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- Tarsius spectrum*, Pl. I., p. 217, Fig. 1, p. 222.  
*Trypanurgus compressus*, Pl. VII., p. 235.  
*Pupaia minor*, Figs. 1-24, pp. 464-468, 471-474, 476-478, 482-485, 487-492.
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# ZOOLOGICAL SOCIETY OF LONDON.

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2. PROOFS AND THEIR CORRECTION.—Two copies of the slip proof, and a page proof for final revision, will be sent to the Author, **but it is important that all serious corrections be made on the slip proof.** Expenses for proof corrections are very heavy, but, if the MSS. comply with Regulation 1, should not exceed 25 per cent. of the printers' charges. If the cost of corrections exceeds 25 per cent., a proportion of the excess will be charged to the Author.

3. Revised proofs must, if possible, be returned within one week from the date of their receipt by the Author.

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# ZOOLOGICAL SOCIETY OF LONDON.

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THIS Society was founded in 1826 by Sir STAMFORD RAFFLES, Mr. J. SABINE, Mr. N. A. VIGORS, and other eminent Naturalists, for the advancement of Zoology and Animal Physiology, and for the introduction of new and curious subjects of the Animal Kingdom, and was incorporated by Royal Charter in 1829.

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The Society consists of Fellows, Imperial Fellows, Honorary, Foreign, and Corresponding Members, elected according to the By-Laws. It carries out the objects of its foundation by means of its collection of living animals, by its Library, and by its Scientific Publications.

The Office of the Society, Regent's Park, N.W.8, where all communications should be sent, addressed to "The Secretary," is open from Ten till Five, except on Saturdays, when it closes at ONE P.M.

The Library, under the superintendence of Mr. F. Martin Duncan, F.R.M.S., F.R.P.S., F.Z.S., is open daily (except Sunday) from Ten A.M. till Five P.M.; on Saturdays, Ten A.M. till One P.M.

The Library is closed from Good Friday to Easter Monday, and upon all other Bank Holidays. It is also closed annually for cleaning during the month of September.

The Meetings of the Society for General Business are held in the Meeting Room at the Society's Office on the third Wednesday of the month at 4.30 P.M. except in September and October.

The Meetings for Scientific Business are held in the Meeting Room at the Society's Office fortnightly on Tuesdays, except in July, August, September, and December and January, at half-past Five o'clock P.M.

The Anniversary Meeting is held on the 29th of April, or the nearest convenient day, at Four P.M.

The Society's Gardens are open daily from Nine o'clock until Sunset, or 8 P.M. when sunset is later. Dr. G. M. Ververs is the Superintendent, Mr. D. Seth-Smith, Curator of Mammals and Birds; Mr. Edward G. Boulenger is Director of the Aquarium; Miss Joan B. Procter, F.L.S., is Curator of Reptiles; Miss L. E. Cheesman, F.E.S., is Curator of Insects; Dr. C. F. Sonntag is Anatomist; Dr. N. S. Lucas, Pathologist; Prof. R. T. Leiper, F.R.S., with the assistance of a panel of experts, examines and reports on the Parasites; Prof. G. H. Wooldridge, F.R.C.V.S., is Honorary Consulting Veterinary Surgeon; and Dr. R. W. A. Salmond, O.B.E., Honorary Radiologist to the Society. Applications for anatomical or pathological material, or for facilities for work in the Prosectorium should be addressed to the Secretary.

#### **TERMS FOR THE ADMISSION OF FELLOWS.**

FELLOWS pay an Admission Fee of £5, and an Annual Contribution of £3, due on the 1st of January, and payable in advance, or a Composition of £45 in lieu thereof; the whole payment, including the Admission Fee, being £50.

No person can be deemed a FELLOW until the Admission Fee and first Annual Subscription of £3 have been paid, or the annual payments have been compounded for.

FELLOWS elected in November and December are not liable for the Subscription for the year in which they are elected.

## PRIVILEGES OF FELLOWS.

FELLOWS have Personal Admission to the Gardens upon signing their names in the book at the entrance gate, and may introduce Two Companions daily.

The WIFE or HUSBAND of a FELLOW can exercise these privileges in the absence of the Fellow.

Until further notice, FELLOWS will receive 40 undated Green Cards, available on any Sunday or week-day up to the end of February of the year following the year of issue, and 20 White Cards available on any week-day up to the same date. Twenty of the Green Cards may be exchanged for a book containing two Orders for each Sunday in the year. Twenty White Cards may be exchanged for a book of dated Week-day Orders, each Order available for any day during the week except Sunday. Special children's tickets are no longer issued, but the Green and White Cards are perforated, and each half is valid for a Child under twelve years of age. It is particularly requested that Fellows *will sign every ticket* before it goes out of their possession. Unsigned tickets are not valid.

FELLOWS are not allowed to pass in friends on their written order or on presentation of their visiting cards.

AQUARIUM.—Fellows have free personal admission to the Aquarium on Sundays and Week-days by signing in the book at the Aquarium Entrance, but this additional privilege cannot be transferred. For the admission to the Aquarium of their friends whom they have admitted to the Gardens personally or by Sunday tickets they may purchase books of 20 tickets for £1, each ticket admitting one adult or two children on Sundays or week-days. Smaller numbers of tickets can also be purchased by Fellows only at the Office, but not at the Aquarium.

FELLOWS have the privilege of receiving the Society's ordinary Publications issued during the year upon payment of the additional Subscription of One Guinea. This Subscription is due upon the 1st of January, and must be paid before the day of the Anniversary Meeting, after which the privilege lapses. FELLOWS are likewise entitled to purchase these Publications at 20 per cent. less than the price charged to the public. A further reduction of 20 per cent. is also made upon all purchases of Publications issued prior to 1881, if above the value of Five Pounds.

FELLOWS also have the privilege of subscribing to the Annual Volume of 'The Zoological Record,' which gives a list of the Works and Publications relating to Zoology in each year, for the sum of Two Pounds Ten Shillings. Separate divisions of volumes 39 onwards can also be supplied. Full particulars of these publications can be had on application to the Secretary.

FELLOWS may obtain a TRANSFERABLE IVORY TICKET admitting two persons, available throughout the whole period of Fellowship, on payment of Ten Pounds in one sum. A second similar ticket may be obtained on payment of a further sum of Twenty Pounds.

Any FELLOW who intends to be absent from the United Kingdom during the space of at least one year, may, upon giving to the Secretary notice in *writing*, have his or her name placed upon the "dormant list," and will then be called upon to pay an annual subscription of £1 only during such absence, or in the event of returning to the United Kingdom before June 30th in any year to pay the balance of the ordinary subscription. After three years a Dormant Fellow must make a further application to be retained on that list.

Any FELLOW, having paid all fees due to the Society, is at liberty to withdraw his or her name upon giving notice in *writing* to the Secretary.

Ladies or Gentlemen wishing to become Fellows of the Society are requested to communicate with "The Secretary."

P. CHALMERS MITCHELL,

*Secretary.*

Regent's Park, London, N.W. 8.  
June, 1924.

**M E E T I N G S**  
OF THE  
**ZOOLOGICAL SOCIETY OF LONDON**  
FOR  
**SCIENTIFIC BUSINESS.**

**1924.**

TUESDAY, OCTOBER ..... 21.

,,      NOVEMBER ..... 4 and 18.

*The Chair will be taken at half-past Five o'clock precisely.*

# ZOOLOGICAL SOCIETY OF LONDON.

## LIST OF PUBLICATIONS.

THE scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are issued in the volumes of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described therein. Amongst such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, paged consecutively, during the months of March, June, September, and December. From January 1901 they have been issued as two half-yearly volumes, indexed separately.

An "Abstract of the Proceedings" is published by the Society on the Tuesday following the date of the Scientific Meeting to which it refers. It is issued along with the "Proceedings," free of extra charge, to all Fellows who subscribe to the Publications, but it may be obtained on the day of publication at the price of Sixpence, or, if desired, sent post free for the sum of Six Shillings per annum, payable in advance.

The "Transactions" contain such of the communications made to the Scientific Meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of One Guinea *before* the day of the Anniversary Meeting, are entitled to receive the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 20 per cent. less than the price charged to the Public. A further reduction of 20 per cent. is made upon purchases of Publications issued prior to 1881, if they exceed the value of Five Pounds.

Fellows also have the privilege of subscribing to the Zoological Record for a sum of Two Pounds Ten Shillings (which includes cost of delivery), payable on the 1st of July in each year; but this privilege is forfeited unless the subscription be paid *before* the 1st of December following.

The following is a complete list of the publications of the Society already issued.



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Since 1916 (Vol. XXI. Part I.) publication of the Society's Transactions has been temporarily suspended, owing to the high cost of production.

In consequence of a re-arrangement of the stock of the 'Transactions,' the Society is now able to offer for sale, at the reduced price of £30, sets of Vols. V.-XVI. inclusive.

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## LISTS OF THE ANIMALS IN THE SOCIETY'S GARDENS.

List of the Vertebrated Animals now or lately Living in the Gardens of the Zoological Society of London. (Eighth Edition.) 8vo. 1883. Cloth, 4s. 6d.

List of the Vertebrated Animals now or lately Living in the Gardens of the Zoological Society of London. (Ninth Edition.) 8vo. 1896. Cloth, 6s.

**CATALOGUE OF THE LIBRARY** of the Zoological Society of London (Fifth Edition.) 8vo. 1902. Cloth, 6s.

**THE OFFICIAL ILLUSTRATED GARDEN GUIDE**—22nd Edition (Revised)—with (1) a Railway and Street Map; (2) a Plan of the Grounds; (3) a short description of some of the principal animals in the Collection, with 52 Photographic Illustrations and Index. Price 1s. in Stiff Paper Cover, postage 2d.

**ZOOLOGICAL RECORD**.—Vol. 59, containing literature relating chiefly to the year 1922, will be published in July 1924, price £3. Vol. 60, for the year 1923, is being prepared as usual, price £3, or subscription, if paid in advance, £2 10s. 0d.

P. CHALMERS MITCHELL,

*Secretary.*

Regent's Park, London, N.W. 8.  
June, 1924.

*These publications may be obtained at the SOCIETY'S OFFICE  
or through any bookseller.*

PROCEEDINGS  
OF THE  
GENERAL MEETINGS FOR SCIENTIFIC BUSINESS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.

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PAPERS.

1. Polychæta of Tropical East Africa, the Red Sea, and Cape Verde Islands collected by Cyril Crossland, and of the Maldivé Archipelago collected by Professor Stanley Gardiner, M.A., F.R.S. By CYRIL CROSSLAND, M.A. (Cantab.), D.Sc. (Lond.), O.N., F.Z.S.

[Received July 25, 1923: Read November 20, 1923.]

(Text-figures 1-126.)

*The Lumbriconereidæ and Staurocephalidæ.*

In 1904 the author was working out a collection made by him in Zanzibar and British East Africa (now Kenya Colony) while working for Sir Charles Eliot, G.C.M.G., F.Z.S., the High Commissioner. Finding that in the state of the literature at that time, certainty of discrimination of species would be assisted by a wider range for examination and being particularly interested in comparing the faunas of the Atlantic and Indo-Pacific areas, he applied to the Carnegie Trustees, who provided funds for an expedition to the Cape Verde Islands. While there he was offered by Professor Herdman a post under the Sudan Government to examine the Pearl Fishery of the Red Sea, and has been engaged there since. This is the origin of the fourth (Red Sea) collection.

The examination of the two former is being resumed after an interval of 19 years, only the Amphinomidæ and Aphroditidæ having been dealt with in the meantime by Mr. Potts.

The present instalment completes the Eunicidæ of the Maldives and East Africa and describes the Lumbriconereidæ and Staurocephalidæ of the four collections.

The following are the genera already described :—

A. In this journal by the present author.

- (1) P. Z. S. 1903, p. 169, two new species of *Phyllochætopterus* from East Africa.
- (2) P. Z. S. 1903, vol. ii. p. 129, species of *Diopatra*, *Onuphis*, *Murphysa*, and *Lysidice*.
- (3) P. Z. S. 1904, vol. i. p. 270—*Chætopterus*, *Phyllochætopterus*, *Hyalinæcia*, *Onuphis*, and *Lysidice*, from the Maldives.
- (4) P. Z. S. 1904, vol. i. p. 287—*Eunice* and *Nicidion* from the Maldives and East Africa.

B. By F. A. Potts, Esq., M.A.: the East African species of Amphinomidæ, Palmyridæ, and Aphroditidæ are incorporated with Prof. J. Stanley Gardiner's Collections from the Percy Sladen Expedition in H.M.S. 'Sealark,' Trans. Linn. Soc. ser. 2, Zool. vol. xii. p. 355, and vol. xiii. p. 325.

The absence from this paper of shaded pencil drawings may be noted. I believe them to be unnecessary to workers familiar with other species of the same genera. The numerous outlines provided can be published at the same cost as a few lithographed plates, and the greater number of illustrations adds much to the value of the work\*. My own experience leads me to believe that future workers will also be grateful to be spared the constant turning over of pages to refer to numbers on plates and back again to their explanations.

It will be noted that I have attempted the description of *species*, not merely of selected *specimens*. The former is a much more difficult and tedious task, but as worms are not postage-stamps the more difficult way is the only one applicable. It has resulted in the discovery of remarkable variations in certain species, while others seem quite stable.

As regards the comparison between the faunas of the two sides of Africa, so far as these few species go they remain distinct.

The British form, *Lumbriconereis latreilli* (= *L. japonica* Marenz.), is represented on both sides, but with slight variation in the Orient. *Arabella novecrinita*, sp. n., ranges from the Indian to Atlantic Oceans, also forming variations in the process. The jaws of this form, like those of *Ænone fulgida* (which appears to

\* It should not be necessary to point out that these small figures are reproduced from larger ones in which detail was carefully considered, in the case of setæ, where necessary, with the aid of  $\frac{1}{2}$ th inch objective and always of camera lucida.

be recorded by Fauvel from West Africa), show remarkable oscillations between symmetry and asymmetry. The genera *Drilonereis* and *Staurocephalus* show no species common to both oceans.

As might be expected, there is a parallelism between Atlantic, Indian Ocean, and Mediterranean species. For instance, *L. heteropoda* ranges from Japan to the Red Sea westwards and to California eastwards, but is not found in the West Indies, where the distinct *L. branchiata* Treadwell takes its place. In these collections *L. debilis* Gr., from the Philippines and Red Sea, seems a parallel to *L. albifrons*, sp. n., from the Cape Verdes. The Oriental *Enone fulgida*, again, is so near the *Halla parthenopeia* of the Mediterranean that the separation of the species into two genera should no longer hold.

The distribution of *L. brevicirra* Schmarda seems anomalous: the species having been recorded only from New Zealand and South Australia, its appearance in the Cape Verdes is unexpected. I have therefore described my specimens in detail in order to provide the means whereby my determination may be corrected if necessary. The species comes near to, but, so far as my material goes, is distinct from, the *L. impatiens* of the Channel.

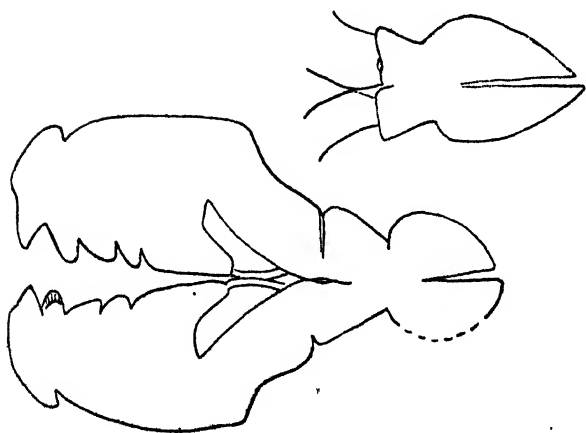
#### Genus LUMBRICONEREIS.

This genus is one of exceptional difficulty, but from the examination of the numerous specimens of these collections (which I divide into seven species, two being new), it is concluded that their discrimination might be easier if authors were to give more attention to features not usually emphasized, *e. g.* the form of the body and *details* of form and structure of the jaw-plates. In many works the characters given will discriminate species locally collected, but are not enough for certainty where the geographical range is the main subject of investigation. The time is not yet ripe for expressing the characters of species of Polychæta as short and simple formulæ, least of all in such a genus as this. This was Grube's ideal, *e. g.* in 1868 and 1869, when he described Ehrenberg's and Frauenfeld's collections from the Red Sea, with the result that, even when other collections from the same area are being examined, not one of his four species can be recognised. Indeed, so far as his descriptions go, they may be *Notocirrus*, *Drilonereis*, or *Arabella*, and not *Lumbriconereis* at all.

Fauvel, Ann. Polych. de Madagascar etc., gives *Lumbriconereis versicolor* Grube, from both Ehrenberg's and Frauenfeld's Red Sea collections, as a synonym of *D. filum* Clp, which he records from Jibuti and Obok, in the Gulf of Aden. Grube's *Lumbriconereis versicolor* is probably a *Drilonereis* or an *Arabella*, but the description omits all mention of the jaws and all details of the setæ, so that it is sheer guess-work to identify it. I did not find *D. filum* either in the Red Sea or at Zanzibar, but in both localities I obtained the new species *Drilonereis major* and *D. logani*.

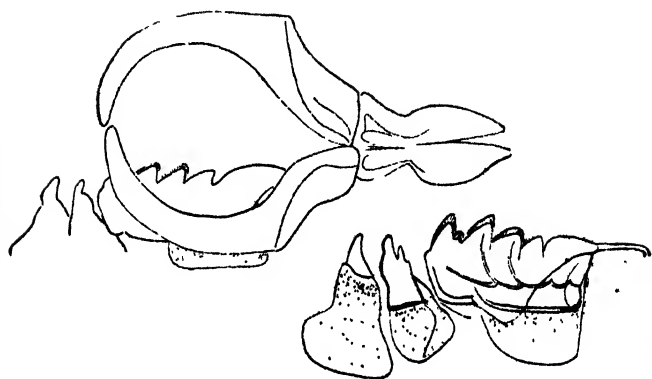


Text-figure 1.



*L. heteropoda*.—Jaw apparatus as seen before bleaching and dissection. (Specimen from Shubuk Suakin.) To right, the supports of another specimen.  $\times 30$ .

Text-figure 2.



Jaws of a Suez specimen as seen after bleaching. Touthed plates of one side removed to the left.  $\times 30$ .



- (4) Upper jaw-plates *black*, not merely a dark brown. Generally similar to other species.

Marenzeller's description, accurate as it is, can be completed from this material, which was collected in the following localities:—

Kenya Colony, Wasin mainland, on shore: 1 large specimen.

Zanzibar, Chuaka Bay, in shore-sand: 3 specimens, of which one was about a foot long, a second six inches by a quarter of an inch when alive.

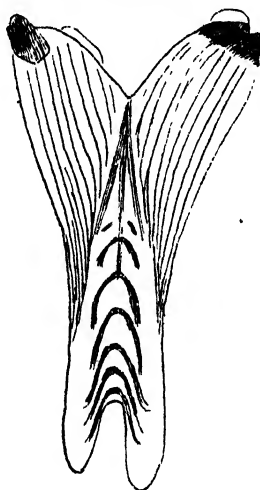
Red Sea, reefs of Shubuk Suakin, 9 fathoms, mud: 2 specimens.

Suez Bay,  $4\frac{1}{2}$  fathoms, mud: 1 specimen.

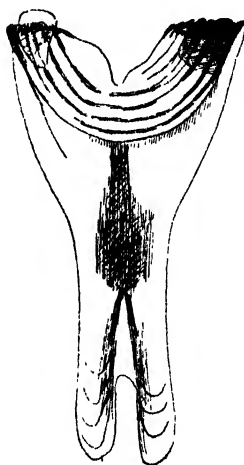
It does not occur in either the Maldivian or Cape Verde collections.

In life the colour is the usual pale flesh tint, one specimen being distinctly red.

Text-figure 3.



Text-figure 4.



*L. heteropoda*.—Surface views, dorsal and ventral, of the mandible of a Suez specimen.  $\times 30$ .

1. *Jaw apparatus*.—Apparently Marenzeller drew his figure of the large dental plates from an opaque specimen. In this species the jaws are so black and opaque that little can be made of them mounted as transparencies for camera lucida drawing. Text-fig. 1 shows such a specimen, to which any details added are really guess-work. After bleaching and softening in NaOH and  $H_2O$ , dissection is possible, and details can be easily seen as in text-fig. 2. The canals found in species with transparent jaws can be easily seen, and the distinction between the homogeneous

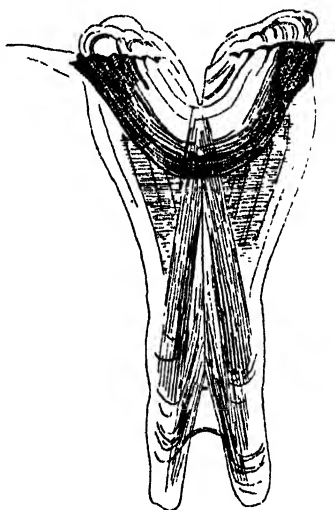
brown material of the plates themselves and the yellow black-spotted accessory plates becomes clear.

I also give a sketch of the supports of a third specimen, as there is some variation in their proportions.

Marenzeller figures only one-half of the lower jaws. Moore describes them but gives only an outline. McIntosh describes them as peculiarly constructed, and Izuka follows him in his comparison of the end-plates to a *Tellina* shell, which I fail to understand.

In the hope of elucidating this I give in text-figures 3 and 4 surface views both dorsal and ventral of a Suez specimen, and the usual transparency of one (text-fig. 5) from 9 fathoms, Shubuk

Text-figure 5.



Mandible seen as a transparency. Note the greater development of the colourless calcareous cutting-edge in this specimen.

Suakin. I take the latter to show greater age in the darker markings and greater stoutness and breadth of the plates, though all are of the same length. The Suez specimen is markedly asymmetrical.

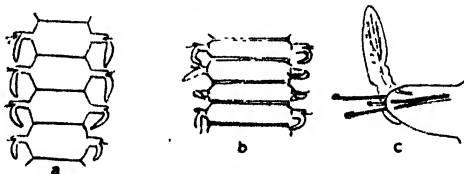
2. *Feet*.—The lip of the seta-sac is stated to project greatly in many species, but on further examination, and where figures are given, it is found that the projection is quite small in comparison with that found here.

McIntosh describes "a considerable triangular area elevated above the foot"; Marenzeller "a long finger-shaped backwardly directed appendage, half the length of the parapodium," his figure corresponding to middle region feet in my specimens.

Marenzeller's specimen was undergoing regeneration posteriorly\*, so that apparently he did not see the full development of this remarkable feature. In undamaged specimens these processes in the last third of the body attain a length equal to that of the parapodium, which is itself peculiarly elongated (see text-fig. 6). They are flattened, generally directed over the back, and sometimes show a constriction where they join the foot. Being highly vascular and evidently functioning as gills, they tend to take the position, relative to the body, assumed by real gills in other Annelids.

These structures justify the specific name *heteropoda*, which is not at all applicable to any other *Lumbriconereis* except *erecta*, not even to the *L. branchiata* of the West Indies, which is somewhat similar. Text-figures 6 a & b show posterior segments expanded and contracted. In my specimens the former condition

Text-figure 6.



*L. heteropoda*.—Feet of the hind region showing the characteristic process of the seta-sac lip.

(a) Segments elongated, feet fully protruded and seta-sac lip lying posteriorly.  $\times 4$ .

(b) Segments contracted, seta-sac lip directed dorsally.  $\times 3$ .

Conditions a and b may be found in the same worm. Fig. a represents an extreme case.

(c) One of the feet of the hind body seen from the fore side with vascular process of seta-sac lip in erect position.

is the commoner, but both may occur in adjacent parts of the same worm. The length of the feet is sometimes lessened by their partial retraction into the body-wall, which explains the only difference between my and Moore's Californian specimens.

This development of the seta-sac lip in the hind body, the most characteristic feature of the species, is not mentioned by Izuka, whose figure again of an uncinata seta differs entirely from McIntosh's, and is not very like Marenzeller's.

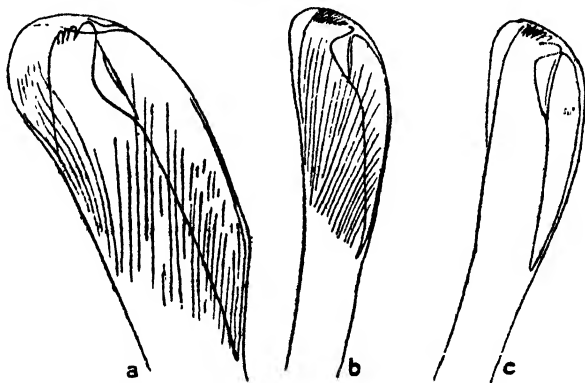
3. *Setae*.—I am not able to find so broad and distinct a distal tooth at the end of the crochet (*i. e.* opposite to the main hook) as is shown in Marenzeller's and Izuka's figures. Moore's figure (for *L. erecta*) shows an extreme development of the broad guards such as occurs in anterior feet (text-fig. 7 a). The posterior setae are more slender and project a long way (text-fig. 7 b). In other respects Moore's figures correspond with my specimens. I give

\* I presume that "*Verjüngend*" may bear this meaning.

three figures of these setæ showing individual variation and that between anterior and posterior feet. In the teeth at the end of the seta the specimen of text-fig. 7c is clearly intermediate between the other two. The fine toothed form is the more common, especially anteriorly. In colour they vary between no colour at all and, in one specimen, dark brown. In this specimen extremes meet, the colourless setæ being apparently ready to replace the old deeply coloured ones.

This is a species of wide distribution from the Red Sea to the Indian Ocean and both sides of the Pacific, Japan and California. It seems significant that it does *not* occur in the West Indies, where its place is apparently taken by the distinct *L. branchiata* Treadwell.

Text-figure 7.



*L. heteropoda*.—Crocket setæ, showing variation.

- (a) Middle region of Kenya Colony specimen. The broad guard is like that figured by Moore.
- (b) From hind end of Zanzibar specimen, finely toothed.
- (c) From middle region of Zanzibar specimen with teeth of intermediate size. All  $\times 320$ .

Moore also records *L. heteropoda* as dredged by the 'Albatros' near Japan, but neither Izuka nor I can agree with his suggestion that it is the same as *L. bifurcata* McL.

The differences are noted by McIntosh, the principal being that in the latter *both* lips of the seta-*anc* are prolonged, a condition carried to an extreme in *L. bifilaris* Ehlers\* from South America. In both *fucata* and *bifilaris* the prostomium is "a somewhat acute cone," quite different from the blunt prostomium of *L. heteropoda*. In life it was noted that the prostomium was very mobile and could be pointed or quite blunt. It is not pointed in any of the preserved specimens, however.

\* Ehlers, 'Polychaeten der Magalhaenischen und Chilenischen Strandes,' p. 139, Berlin, 1901.

LUMBRICONEREIS LATREILLI Aud. et Edw. 1843.

*L. japonica* Marenzeller, "Süd-japanische Anneliden," Denk.  
Kais. Akad. Wiss. Wien, 1879.

„ McIntosh, 'Challenger,' vol. xii.

„ Izuka, *l. c.*

„ Moore. Acad. Nat. Sci. Philadelphia, 1903.

„ Treadwell, Carnegie Inst. Wash. No. 312, 1922.

*L. latreilli* De St. Joseph, Ann. Sci. Nat. 1898.

„ McIntosh, Brit. Annelids.

„ Fauvel, Arch. Zool. Exp. et Gén. 1919.

*L. naruta* Treadwell, Carnegie Inst. Washington, xv. 1921.

These collections provide a series of examples from giants 5 mm. in diameter (Minikoi) to minute examples of 0.5 and less, from both the Atlantic and Indian Oceans.

We thus have material for :—

- (1) Understanding the inclusion of the 'Challenger' specimens in Marenzeller's species in spite of wide differences of setæ and jaws.
- (2) A study of variation.
- (3) The study of the marked changes which occur during growth.
- (4) The study of the differences between Atlantic and Indian Ocean varieties.

By the kindness of Dr. E. J. Allen, F.R.S., F.Z.S., Director of the Laboratory at Plymouth, I have been enabled to make a detailed comparison between these collections and specimens from the English Channel.

Special attention to minute detail has been necessitated not only by the variation between individuals of different sizes and of the two sides of Africa, but by the close relationship between *L. latreilli* and other species. For instance, Willey\*, in referring to this species (under the name of *L. nardonis*), writes: "Almost the only difference (the only one which I can recognise) between *L. coccinea* and *L. nardonis* relates to the form of the prostomium, which is subglobular in the former and subconical in the latter." He mentions also the greater breadth of the body anteriorly in *L. coccinea*. In fact, previous descriptions of the species omit much of interest, and the figures published are too few and often too rough for this difficult genus. The necessity for accurate detail is specially emphasized here by the occurrence, in single individuals of medium size, of most of the types of seta found in the genus, and to these several others are added by the largest and smallest examples. The generalised character and variability of the jaw apparatus deprive us of the help which these organs might have been expected to give.

\* "Littoral Polychæta from the Cape of Good Hope," Trans. Linn. Soc. vol. ix. 1903-7.

*Short description.*

Body narrowed anteriorly, the broadest part being 10-15 segments behind the head. Round, slightly flattened ventrally.

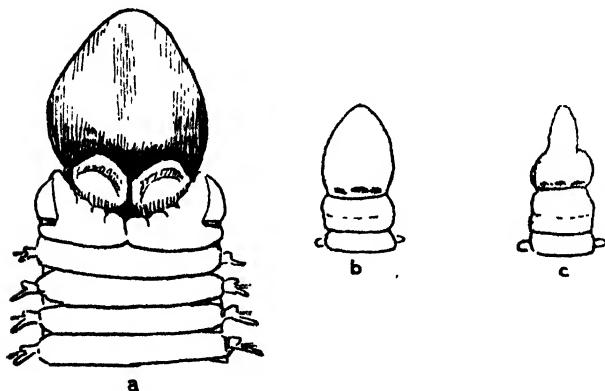
Prostomium bluntly conical, longer than broad, generally smooth and more or less round in vertical section (text-fig. 8a.)

Jaws of a generalised type, usually 4 teeth on each of the large plates; supports often broad, pointed and more or less frayed behind.

Feet well developed throughout the body; process of seta-sac lip conspicuous, but more so in posterior segments than in anterior.

Setæ comprise capillaries, jointed compounds and unjointed crochets, besides aciculæ. The heads of compounds are longer

Text-figure 8.

*L. latreilli.*

(a) Prostomium and fore body of a preserved specimen, ventral view.  $\times 15$ .

Palps (or "mundpolster") thrust forward by beginning of eversion of jaws.

(b) & (c). Rough sketches of dorsal aspect of the living worms, in (c) contracted.

All three from Cape Verde Isl. specimens.

anteriorly, shorter posteriorly, but their proportions vary greatly with the size of the specimen. Their heads, like the crochets, bear one large tooth with smaller denticulations above it. These vary in number and distinctness. Compound setæ disappear about the 20th foot and are replaced by crochets, which continue to the end of the body. To about the 40th foot they are accompanied by a few capillaries, thereafter are found alone.

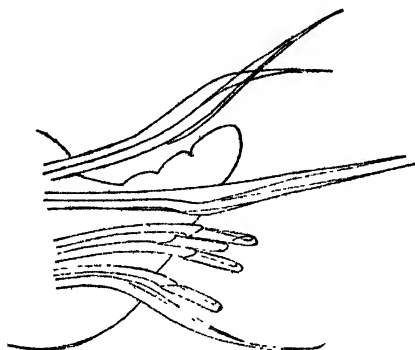
The specimens from the Cape Verde Islands agree closely with those from Plymouth, but the Oriental examples constitute a distinct variety (possibly two varieties) and will be described in detail later.

Three specimens were collected from among nodules of litho-

thamnia at 3 fathoms in St. Vincent Harbour, all small, 1.5 mm., 1.1 mm., and 0.6 mm. in diameter respectively.

One from digging in white shell-sand on the shore of the Island of Sal and several small from "washings."

Text-figure 9.



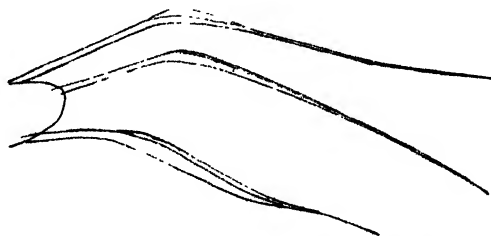
*L. latreilli*.—10th foot showing sinuous and straight capillaries.  $\times 100$ .

The species is apparently far less common in these localities than the next to be described.

The colour in life is described as bright pink; no pigment except a few spots on the base of the dorsal surface of the prostomium, too irregular to be eye-spots.

In the smallest specimen from St. Vincent there did appear to be minute grains of reddish pigment *in the skin* which left the

Text-figure 10.



23rd foot showing full development of the straighter setae, together with the single ventral seta. The angle between head and shaft varies in adjacent feet.  $\times 100$ .

intersegmental grooves colourless. Posteriorly the colour became yellowish.

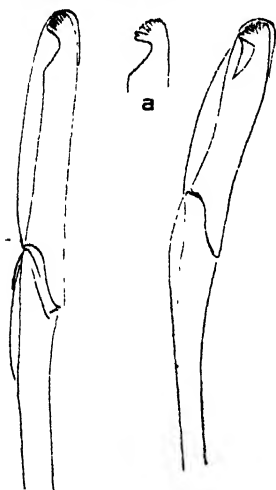
The worm is active, and the prostomium may contract as shown in the sketch (text-fig. 8*b, c*) as a result of handling. This

rough sketch shows, however, that there is but little change of shape on killing in fresh water and spirit, though there is great contraction of the body, the original length being halved (text-fig. 8 a).

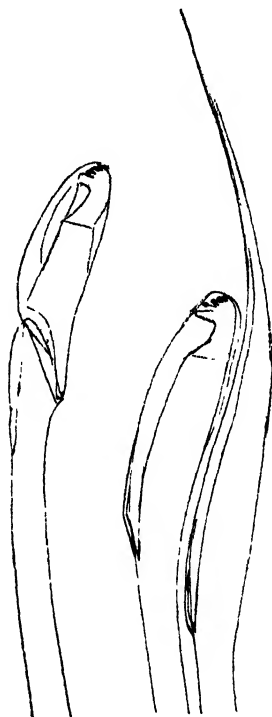
The form of the body, prostomium, jaws, etc. are described sufficiently under var. *japonica*, but attention is directed here to details of the setæ, which have not hitherto been described, though they agree well with British specimens. Among the capillary

Text-figure 12.

Text-figure 11.



*L. latreilli*. — Long and medium-headed compound setæ from 10th and 20th feet. Note marked variation in the teeth. Fig. a shows the commonest type of head and denticulation.  $\times 320$ .



Three setæ of 27th foot—viz., short-headed compound, intermediate form of crochet and ventral capillary.  $\times 200$ .

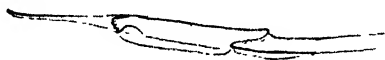
setæ two kinds can be distinguished—the rather broad, sinuous form characteristic of the two dorsal and single ventral of each foot, and the straight-headed pair next to the compound setæ in the dorsal bundle. All are narrowly bordered, but in the second form the border is confined to a short portion at the base of the head. Their normal forms are shown in text-fig. 9, which shows the setæ of the 10th foot.



In the region between the 20th and 25th feet this pair sometimes becomes very prominent and the heads are often bent at an angle with the shaft; text-fig. 10 shows an especially conspicuous pair.

The compound setæ may be roughly divided into long, medium, and short headed, the former being found between feet 5 and 17, the medium before 5 and from 18 to 21. In the 21st foot

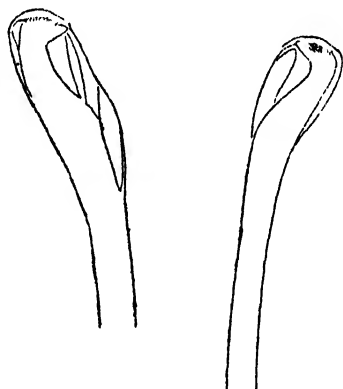
Text-figure 13.



The *Orychata* variety of seta, from 10th foot.

medium and short-headed setæ are found together, as are long and medium in the 17th, but from 20th to 25th short heads occur alone. In the 25th foot an unjointed crotchet appears in place of one of the compound setæ; the latter disappear in the next foot, which, like all as far as the 40th or thereabouts, bears a few capillaries and crotchets only. These capillaries dwindle in number and size and die out in the region of the 40th foot, after which 3, sometimes 4, crotchets occur alone to the end of the body.

Text-figure 14.



*L. latreilli*.—Crochets of posterior feet, thick and thin from one foot. Denticulations differ markedly.  $\times 240$ .

Text-figs. 11 and 12 give details of these compound setæ. It will be noticed that while there is considerable variation in detail, the characteristic form of the head is preserved and that the denticles it bears consist of one rather square-ended tooth with five denticles above it. In certain cases the large tooth itself appears to be split.

In a single specimen, one dredged from 3 fathoms off Bon

Vista Island, one seta was found having an elongated end to the guard as shown in text-fig. 13. The occasional occurrence of compound setæ with this feature characterises *L. oxychota* Gravier from the Red Sea, which is otherwise very like *L. japonica* Marenz.—the present species—but appears to differ in the prominence of its prostomium, length of setæ, and details of the heads of compound setæ and hooks. Also a specimen the size of Gravier's, 0.95 mm. in diameter, would hardly have compounds with such long heads as those figured if it were really of this species. The occasional appearance of this structure in *L. fragilis* is figured by McIntosh, Brit. Ann. pl. lxxxii. fig. 2 b.

Text-fig. 12 shows the transition form of the crochets, which, while figured as characteristic of the crochets of other species\*, has not been described in *L. latreilli*, though I find it in all specimens, including those from Plymouth. It occurs only in a few feet about the point at which the compound setæ disappear, after which the more normal form takes its place (text-fig. 14).

These crochets are all very finely denticulated, generally the drawings are comparatively coarse. In many cases they are continued into the upper surface of the large tooth so that its individuality is lost. In all the posterior feet the three crochets are thick, medium, and thin, of which the first and last are shown in text-fig. 14.

The wings, or hoods, vary in both length and breadth.

#### *L. LATREILLI* var. *JAPONICA*.

(= *L. japonica* Marenzeller.)

The following are included.—

From Equatorial East Africa:

Wasin, 10 fathoms, fragments of 6 small specimens.

Chuaka, Zanzibar, between tide-marks, 1 specimen.

From the Maldives:

Hulule, Male Atoll, 7 largest specimens, 5 mm. broad.

Minikoi, 1 of 1.5 mm.

Red Sea, Suakin Harbour, 2 specimens.

Suez, by J. Gordon Logan, Esq.: 1 hind end.

„ by C. C.: Dock walls among *Margaritifera vulgaris*, 1 specimen.

*L. nasuta*, Verrill, described by Treadwell from the West Indies, is 4.4 mm. broad and resembles, in structure as well as in size, the above specimen from the Maldives. It is curious that *L. latreilli* does not occur among the eight species Treadwell describes; *L. floridana* is nearest, but has compound setæ alone in the first ten feet, and in none of the eight species are the different types of these setæ—or of the capillaries—described.

\* McIntosh, 'British Annelids,' pl. lxxxii. for species *fragilis*, *impatiens*, *hibernica*, and *laurentianus*. I do not find any of the posterior crochets so sharply bent or distinctly denticulated as McIntosh's text-fig. 8 c (of *L. latreilli*) in any of my specimens from the Cape Verdes or from Plymouth.

The specimens described by Marenzeller and by McIntosh are widely different, especially in the compound setae, which are very long-headed in McIntosh's figure, rather short and broad in the original by Marenzeller, and in the jaws, of which the supports are extraordinarily short in the 'Challenger' example and of average proportions and no particular distinctive character in Marenzeller's. Izuka seems to follow McIntosh rather than Marenzeller, though the one seta he figures differs from either, and his drawing of the foot omits the characteristic extension of the dorsal corner of the seta-sac lip.

From the examination of a series of specimens of all sizes I conclude that most of the differences are due to the species being of peculiar variability and to the fact that, while the type was described from a specimen 2 mm. wide, those obtained by McIntosh and Izuka (and Treadwell) were 7 mm., 6 mm., and 4.4 mm. wide, i. e. of about nine times the bulk. Though specific identity has been established, it is not certain whether these large specimens should or should not be made a named variety.

No author has yet described, still less figured, the interesting variability shown, and this should have been done fully before the identity of species of these large specimens with the original of Marenzeller had been accepted, or, in these collections, the large specimens from Male Atoll and Suakin Harbour with those of East Africa, other parts of the Red Sea, and the Cape Verde Islands. Even though the species has been known so long from the Channel, etc., a really complete and accurate description of variation has not yet appeared.

To form a basis for a description of the changes of structure with size, and for comparison with the other variety and closely related species, a single specimen is first described in detail. For this purpose the larger of two specimens from Suakin Harbour is selected as being of medium size—2.5 mm. maximum breadth without the feet—and having undamaged setae.

The proportions of the body are given by text-figs. 15 to 17, which show the rapid taper at the head end. The body in this region is very muscular, but less so after the 10th segment, where it narrows slightly, to expand again to its maximum, which is shown in text-fig. 17 about the 50th segment. Posteriorly, as is usual, muscularity decreases and segments become somewhat longer, but they do not lengthen conspicuously as in some other species. There is a gradual taper to the tail, which has cirri long for this genus. I find only three, all of the same length, in this specimen.

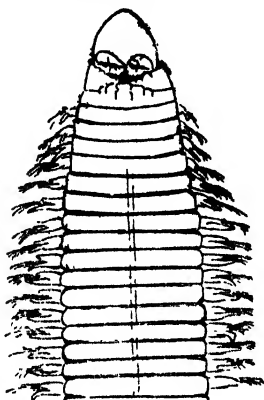
The body is round in section, only slightly flattened ventrally, but flatter in the posterior third.

The prostomium is somewhat egg-shaped thin end forward, longer than broad and round or nearly so in transverse section, quite smooth dorsally and ventrally. It bears two minute pits usually just under the edge of the peristomium, but no other sense organs (these are shown in text-fig. 16 by drawing the

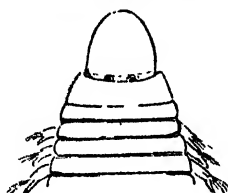
prostomium slightly forward). The "mundpolster" are conspicuous in this specimen, and show a transverse wrinkle.

The peristomium has the proportions shown, and in this specimen its relations to the mouth are a little abnormal, in that the second segment forms so short a portion of the lower lip.

Text-figure 15.

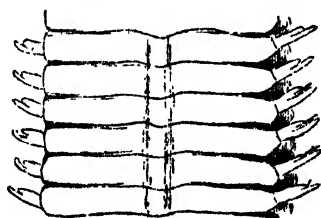


Text-figure 16.



*L. latreilli* var. *japonica*.—Dorsal and ventral views of the anterior end of the Suakin specimen. Protrusion of the "mundpolsters" and peristomial border of the mouth are somewhat exceptional in this specimen. In dorsal view the prostomial pits are visible.  $\times 12$ .

Text-figure 17.

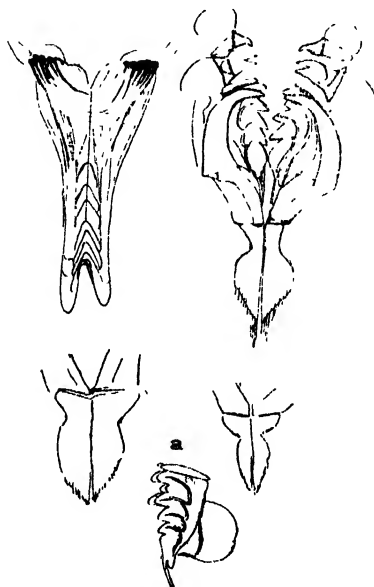


Ventral view of body about 30th segment tilted up on right side to show the feet.  $\times 12$ .

The upper jaws (see text-fig. 18, from East African specimens) are dark brown in colour and of quite general pattern, the teeth being 4—? 5 : 2—2 : 1—1. The raised head of the large plate is somewhat short, pincers slender and well curved. In a side view the base of the pincers and their junction with the supports are seen to be bent ventralwards, the points and the supports

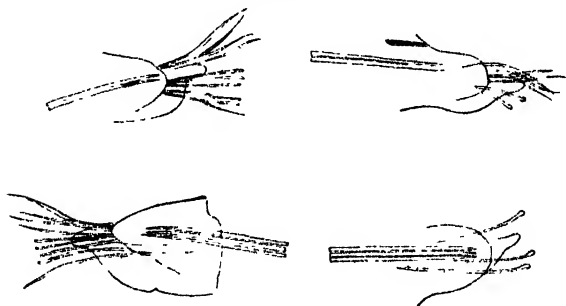
dorsalwards. The supports are short, pointed posteriorly, and frayed along their posteriorly edges.

Text-figure 18.



*L. latreilli* var. *japonica*.—Jaw apparatus. Supports of two other specimens are drawn below to show range of variation in shape. (a) One of the large plates removed to show head, side-plate and calcareous additions to teeth.  $\times 30$ .

Text-figure 19.



Feet: 6th, 20th, 30th, and 50th.  $\times 26$ .

The lower jaw is glassy and has little colour except the brown marks resembling the graining of timber and the black-dotted

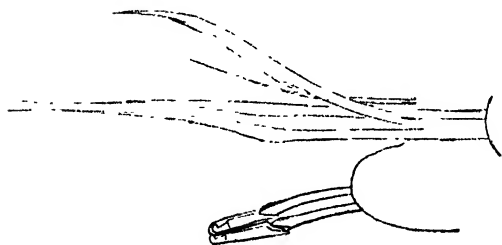
anterior edge, in which features, as well as in the general proportions of the plates, there is but little difference to *L. heteropoda* and other species.

The feet (see text-figs. 15, 17, & 19) are comparatively well developed throughout the body, largest in proportion to the breadth of the body in the first 20 segments. The posterior lip of the seta-sac forms a finger-shaped process from the first foot. This soon projects beyond the foot for a distance equal to half the length of the foot, but it never approaches the development of *L. heteropoda*, and is no more evident posteriorly than it is from the third or fourth segment.

Text-figure 20.



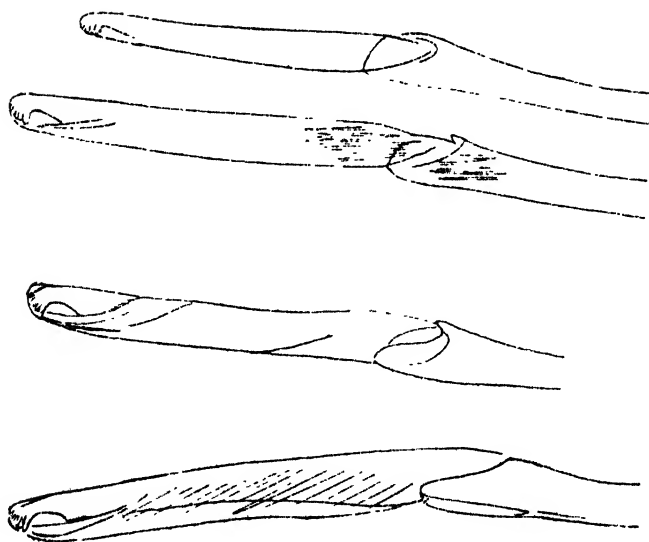
Text-figure 21.



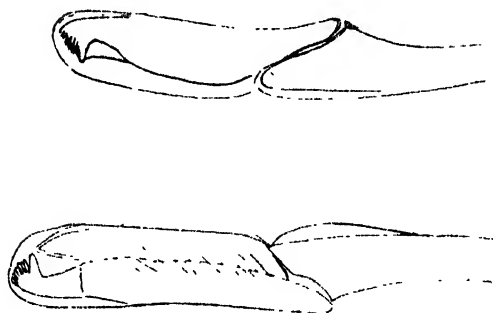
Dorsal capillary setae from 6th and 20th feet.  $\times 100$ .

The setae, in these anterior segments only, are numerous and long, projecting a long way beyond the foot in a beautiful fan. Simple and compound forms occur together from the first foot (which McIntosh remarks is distinctive of the species *L. latreilli*, though *L. coccinea* shows the same feature). The capillaries are slender, narrowly winged with very fine elongated tips, and finely striated. I can find none like that figured by Marenzeller, sharply bent with broad wings (text-figs. 20 & 21).

Text-figure 22.

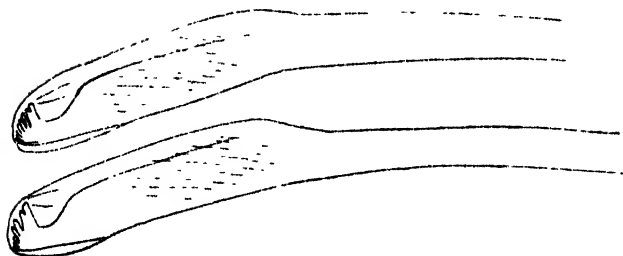


Text-figure 23.

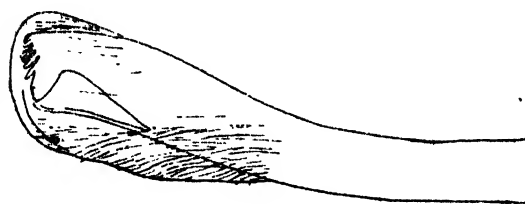


Compound setae showing variations in size and shape and large and small teeth of heads. Left to right : One from 10th foot, three from 6th, and two from 20th. Latter pair from opposite sides of the body.  $\times 900$ .

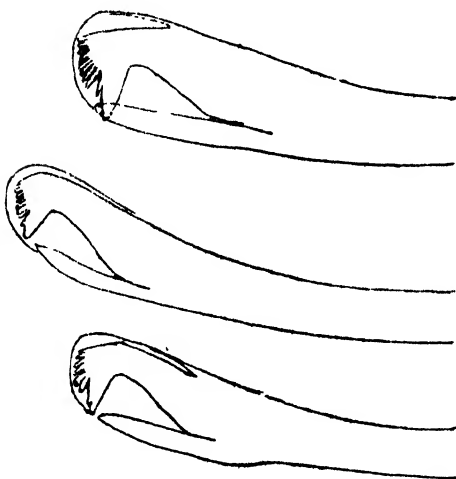
Text-figure 24.



Text-figure 26.



Text-figure 25.



Crochet -etee. Left to right a pair of the intermediate form from 30th foot, the three crochets of 65th and one large crochet from 85th foot.  
 Figs. 24 & 25  $\times 200$ . Fig. 26  $\times 320$ .



The numbers found are :—

Foot 6	Capillaries 4	Compounds 6	Capillary 1	Aciculæ 2
„ 10	„ 6	„ long 8	„ 1	„ 3
„ 15	„ 5	„ med. 9	„ 1	„ 4
„ 18	„ 4	„ 6		„ 3
„ 20	„ 5	„ 4	„ 1	„ 2 or 3
„ 25	„ 4	„ 4	„ 1	„ 2
„ 30	„ 3	Crochets 3	—	„ 2
„ 40	„ 2	„ 3	—	„ 2

Of these capillaries two patterns may be distinguished, though not so clearly in this specimen as in others. The dorsal and ventral units are broader than the others, and more sinuous, the ventral the shorter. The two ventral of the dorsal bundle are less sinuous and more sharply bent, if at all, have more conspicuous but shorter wings, and end in very long attenuate tips. These variations can be followed through the series of feet, but are more clear about 20–25. The wings are narrow in all cases, but in many hardly visible at all.

The compound setæ are peculiarly variable. In the first ten feet or so they have heads of a very elongated form with narrow, often scarcely distinguishable, borders. The hoods have frequently a curious appearance of having fallen away from the heads. They are striated, the striæ ending in very minute denticles along the border, too fine for the drawings, though these were made under  $\frac{1}{2}$  objective. They are indicated in the middle outline of text-fig. 22 at the collar-like upper edge of the hood.

Further back the heads are shorter, or more like that figured by Marenzeller, though the correspondence is far from exact (text-fig. 23).

Variations in the fineness of the teeth at the ends of the heads is shown in text-fig. 23, where the example to the right bears teeth so fine that their shape is not given in the drawing.

These short-headed compound setæ are few, for they appear only a few segments before compound setæ disappear altogether, which is about the 26th foot. This contains six capillaries and hooked crochets only, the former disappearing about the 40th foot, after which three or four crochets are all that the foot carries to the end of the body.

These crochets vary as widely among themselves as do the drawings given in various works by which species are supposed to be discriminated. Compare text-figs. 25 and 26, in which variations are shown in

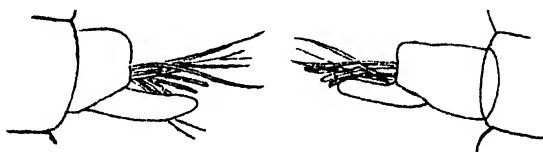
- (1) prominence of the large tooth ;
- (2) of the denticles behind it and of those upon it ;
- (3) the guard ;
- (4) size and curvature of the seta.

As regards the denticles upon the large tooth, text-fig. 24 shows almost a doubling of the big tooth; text-fig. 25, the seta to the right a long narrow tooth at its base and two near its point, which latter are so small as to resemble slips of the pen. In the setæ of hinder segments (text-fig. 26) these denticles, except the long one near the base, are scarcely visible.

The difference in thickness, etc. of the three crochets shown in text-fig. 25 is repeated in every foot, but the breadth of guard shown in text-fig. 26 is an occasional feature.

*Specimen No. 2.*—Collected with the above, but smaller, being only 2 mm. wide. The "mundpolsters" and lower lip are normally developed, and the two pits on posterior part of prostomium are more deeply covered by the peristomial border. Otherwise exactly like No. 1, as are body proportions and feet (text-fig. 27), except that posterior feet are shorter.

Text-figure 27.



*L. latreilli* var. *japonica*. Specimen no. 2. On right, 12th, and on left, 18th feet, seen from above.

Setæ, four compounds, rather short-headed, in first foot, long-headed to 14th foot, then shorter to 21st. Capillaries to about foot 30.

The slenderness and other peculiarities of the long-headed compounds are here much less extreme, the intermediate short-headed being much as in No. 1, but seem to occur in a greater number of feet (see text-fig. 28).

Crochets of the type of foot 30 in specimen No. 1 are found only in feet 20–25. In the 50th foot (text-fig. 29) one seta has broad guards like No. 1, foot 85, with heads like those of foot 55 in specimen 1.

70th foot and in fragment of posterior end crochets are of the fine-toothed type.

*Specimen No. 3.*—Red Sea, Stn. 44, from among pearl-oysters (*M. vulgaris*) from the dock-wall at Suez.

Maximum breadth 1.5 mm.; longest feet, including finger-like projection, 0.5 mm.

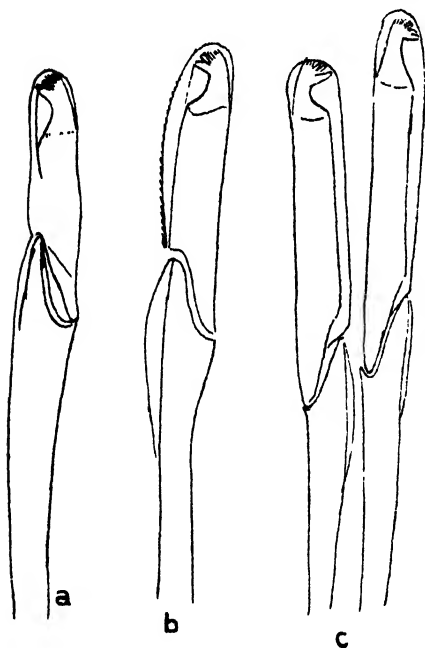
Pro- and peristomium, feet and body proportions agree with the above, but for the trifling differences that the body is a little flatter and the posterior feet are perhaps more prominent, an appearance possibly due to better preservation.

The compound setæ of anterior feet are like those of No. 2,

but about foot 20 they are very short-headed. The three types found are figured (text-fig. 80). This last seta is like that figured by Marenzeller, but differs in detail, and especially in size, these two drawings being of about the same magnification [this is  $\times 300$ , Marenzeller's  $\times 330$ ]. Crochets appear to be all of the fine-toothed type.

No. 4.—A series of specimens of 1.4 to 1.6 mm. in diameter, from 10 fathoms, Wasin, Kenya Colony, and 3 fathoms, Chuaka Bay, Zanzibar.

Text-figure 28.



Text-figure 29.

Crochets of foot 50.  $\times 310$ .

*L. latreilli* var. *japonica*.—Compound setae. a & b, medium and short-headed from 10th foot; c, long-headed from 9th foot.  $\times 240$ .

The only difference noted in body proportions, etc., is that in some of these the feet appear much less prominent than usual, especially posteriorly, an effect which is probably due to the bodies being swollen by genital products\*.

Of these, specimens corresponding with No. 3 in size correspond

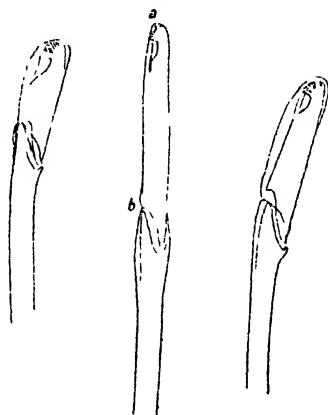
\* It need hardly be remarked that sexual maturity is frequently found long before full size is attained in many invertebrates: e.g., the pearl-oysters, both *M. vulgaris* and *M. margaritifera*, produce eggs and sperm in their second year, their mature ages, as regards size, being 3-5 and 5-10 years respectively.

also in setæ, capillaries, compound and crochets. The head of the shortest crochet resembles Marenzeller's figure in shape, but is again only half the size.

There are but few of the extreme types, of the longest before the 10th foot, and of the shortest one example from about the 20th (text-fig. 31).

No. 5.—In the smallest specimens, 1 mm. in diameter\*, the heads of compound setæ are all alike short, and at the same time the denticles they bear are few and distinct (text-fig. 32), and some capillary setæ appear to be broader winged. This distinctness of the denticles is shown also by some of the crochets in one specimen (text-fig. 33); in others they are quite like those found in larger examples.

Text-figure 30.



*L. latreilli* var. *japonica*.—Specimen no. 3. Long, medium, and short-headed compound setæ from 6th, 16th, and 20th feet.  $\times 300$ .

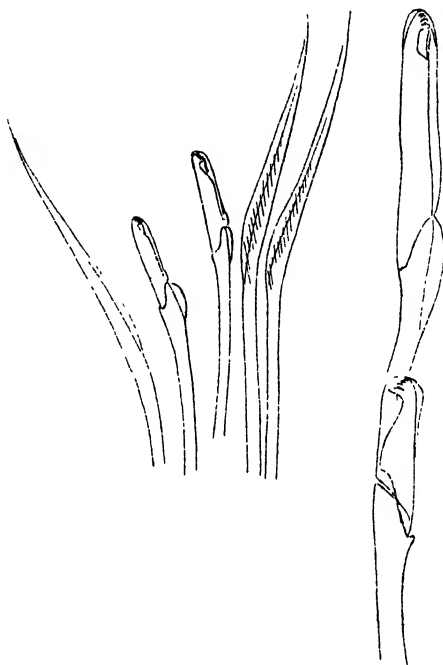
But for the existence of intermediates the setæ of type 5 would clearly differentiate it as a distinct species, in spite of the fact that in the characters of the pro- and peristomia, body proportions, jaws, and structure of the feet the agreement with the other specimens is complete. The proportionate smallness of the feet was noted above.

No. 6.—This descending series is completed by a specimen, 0.5 mm. wide, from Wasin, 10 fathoms, which is mounted whole as a microscope-slide.

It is remarkable that though the crescentic marks of the

\* It will of course be borne in mind that the difference in size between a specimen 1 mm. wide and another 1.5 mm., is not proportional to these numbers, the latter having more than twice the area of cross-section and, roughly,  $3\frac{1}{2}$  times the bulk of each segment.

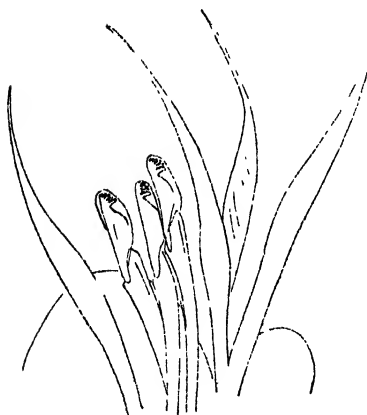
Text-figure 31.



Specimens of series 4. Setae of 10th foot.  $\times 150$ .  
 Longest and shortest compounds from 5th and 20th feet.  $\times 300$ .

Text-figure 32.

Text-figure 33.

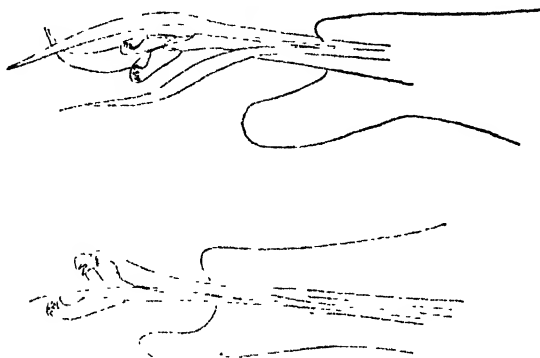


Series 5. Setae of an anterior foot.  
 $\times 275$ .

Ditto. Crochets of one of the  
 posterior feet of the same specimen.

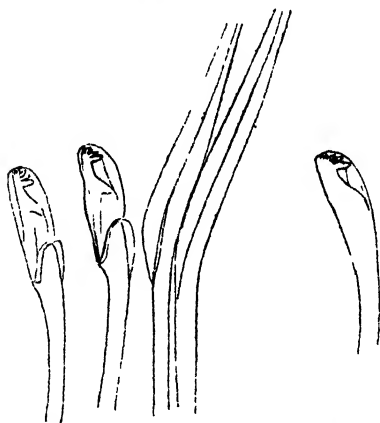
anterior end of the mandibles are clearly visible, nothing can be seen of the eventually much darker maxillary plates. The muscular bulb is well developed and extends back as far as the 5th setigerous segment.

Text-figure 34.



Specimen 6, the smallest specimen of *L. latreilli* var. *japonica*.  
Feet 7 & 16.  $\times 300$ .

Text-figure 35.



Ditto. Details of setae of 10th foot. To right a crochet from 13th foot.  
Compare these in fig. 34.  $\times 300$ .

Compound setae occur from the beginning (owing to breakages the first is visible in the 3rd foot). All are short-headed, and most have two or three distinct teeth, others finer and more numerous denticles (text-fig. 34). The first crochet (text-fig. 35)

appears in foot 9, and the compounds disappear in the next, the last capillaries in 20. The last five of these feet contain only one short and narrow capillary.

The crochets are recognisably the usual type but simplified, consisting generally of the large fang and two smaller teeth above it, the numerous small teeth above these not being yet differentiated.

We have thus a clearly continuous series showing the great change in these setæ with increase in size of body. The capillaries, which are of very generalised type, show nothing corresponding; some setæ in smaller examples are broader in proportion to length, but in the whole series I find none so broad and sharply bent as Marenzeller's figure. Those drawn include, in all cases, the broadest winged.

The jaw apparatus provides hardly any diagnostic character,

Text-figure 36.



Jaws of a small specimen from series 4.  $\times 60$ .

except the frayed appearance of the lower part of the supports. In general the specimens are alike (compare text-fig. 36 with text-fig. 18), but the characters shown are all shared by other species. The sculpturing and canals of the large plates, which are striking features, are prominent in any others which are sufficiently transparent to show them; the raised heads of those plates, overlapping the points of the pincers, are common, and so are the shape of the lower angles of these and the characters of the upper plates. The supports are variable in shape, as shown by the three specimens from East Africa and the smaller from Wasin, in which there is a broadening of the bases of the pincers shown to a lesser degree in other specimens. The beginning of this feature appears on the left only of the first specimen figured. Evidently this variation is individual and not connected with age.

The numbers of teeth on the large plates are:—

- Specimen 1. 5—5.  
 „ 2. (not dissected).  
 „ 3. 5—6.  
 „ 4. 5—5. 5—6. 4—4.  
 „ 5. 3—4. 4—4.  
 „ 6. (not developed).

The higher numbers are clearly due to additional small teeth developed in some older specimens, as shown in text-fig. 18*a*, where the plate has been dissected away from forceps, etc. so that details of the head are visible. There is sometimes a small tooth also above the edge of the upturned head.

In plates separated from the pincers it is curious to notice that the strong brown toothed part, bounded by the vertical line of the canals, is separated by a nearly transparent portion from the accessory plate to the right which is rendered dense by the usual dots of black chitin.

The lower jaws are also of a common type. The figure shows the black and brown markings, which would aid the definition of the species were they always visible, but in smaller specimens they are very faint or non-existent. In this case they correspond closely with Marenzeller's specimen.

The differences shown by the seven large specimens from Hulule, Male Atoll are now explicable.

These are all of about the same size, 5 mm. wide, that is to say about six times the size of the largest of the preceding series.

As would be expected, the compound setæ are all elongated (text-fig. 37). In spite of the fact that unbroken setæ are rare, the finding of the first crochet (about foot 25) together with long-headed setæ as shown in text-fig. 38, proves that no shorter exist in this region, and one long-headed seta exists in a second foot. The extreme form found in anterior feet is shown in text-fig. 37, with the broadest which accompany it. The degeneration (they are not worn) of the denticles and elongated neck is noticeable.

The first crochet of the 25th foot is comparable to those found in the corresponding position in the Suakin specimens, but is narrower and has a more elongated neck and smaller teeth.

In posterior feet the same change of shape and of the wings occurs as in former specimens.

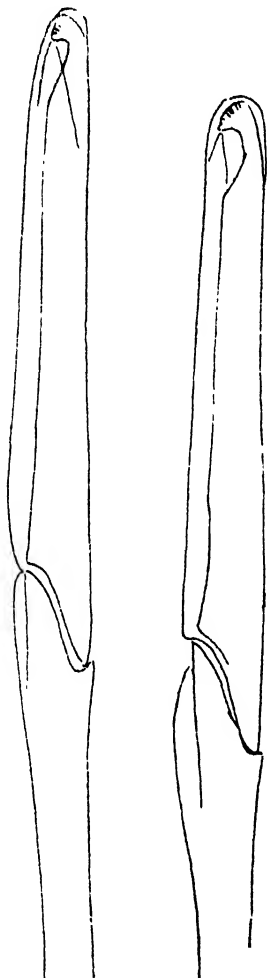
A very striking difference is seen in the acicula of these hinder feet, as it is jet-black (text-fig. 39). Hitherto we have had only yellow aciculæ, even in posterior feet, or at most, brown-tipped. Here they are yellow in anterior feet: in foot 20 there are five aciculæ, of which one is brown; in foot 30 there are six, of which two are brown.

In the prostomium, proportions of the body, structure of feet, and the capillary setæ and jaws there is no difference to record,

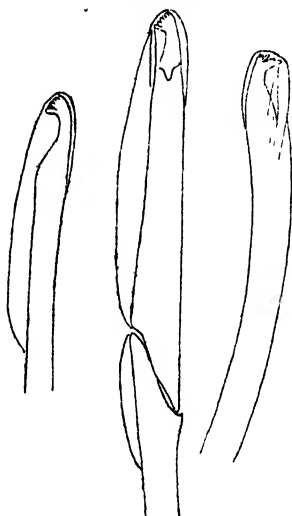


except that the dorsal process of the seta-sac lip is distinctly more developed, and there are six capillaries in the dorsal bundle.

Text-figure 37.



Text-figure 38.



*L. latreilli*. Maldivan specimens.—On left: Compound setae from 15th foot. Next: Intermediate form of crochet and long-headed compound, both from 25th foot,  $\times 300$ . On right: Crochet from a posterior foot,  $\times 150$ .

The jaw-plates are dark brown, but the "canals" can be made out. Variations in the supports similar to those of the smaller

specimens occur, and the breadth of the angles of the pincers at their articulation varies in the same way (text-fig. 40).

The lower jaws, as would be expected, all show clearly the three sets of brown lines characteristic of the species.

In specimens mounted in balsam 19 years ago the calcareous matter seems to have disappeared, but in one mounted this year it is present in normal proportions.

The specimen from Minikoi has lost all its setæ except a few capillaries and crochets, these and the structure of the feet and jaws justifying its inclusion in this species. It differs from all other examples in the straighter sides and more pointed outline of the prostomium, which bears deep but narrow grooves not only in the mid-dorsal and ventral lines, but laterally on both surfaces. The two rings of the peristomium are both short and of equal length; the lower lip is but slightly wrinkled. Anterior feet scarcely project, a feature which is structural and diagnostic in some species, but in this case is visibly due to retraction. In fact, all the above peculiarities may perhaps be attributed to the method of preservation.

Text-figure 39.



One of the hinder feet with black acicula.  $\times 35$ .

The posterior points of the supports of the jaw apparatus are peculiarly long.

We have thus proved that what appeared to be three species are but stages in the growth of one.

The var. *japonica* of the Indo-Pacific is distinguished from the type of the species by—

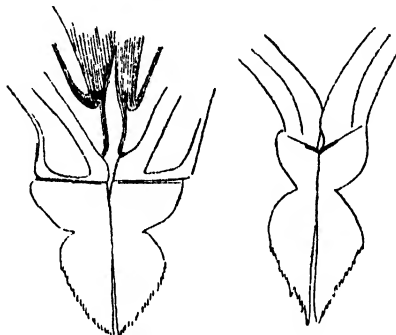
- (1) The great size it may attain, *i. e.* 5 to 7 mm. across the body without the feet. This is accompanied by still further elongation of the heads of the compound setæ and absence of the shorter and medium heads.
- (2) Slightly greater numbers of setæ per foot.
- (3) The distinctness of the big teeth on the crochets and heads of compounds, and coarseness of the denticles above the big tooth.
- (4) Less conspicuous characters of the middle capillaries of the feet about the 20th.

The smallest specimens from either ocean differ in having fewer setæ of all kinds, shorter heads to the compounds with fewer and more distinct denticles on them as on the crochets,

while the capillaries are more broadly winged. These differences would place them in a distinct species did not intermediate stages exist leading up to typical specimens. As would be expected, the change in characters of setæ occurs earlier in the body, in specimens 0.5 mm. wide, *i. e.* as early as the 10th foot.

The table of these variations brings out their connection with size quite clearly.

Text-figure 40.



*L. latreilli*. Maldivan specimen.—Extremes of variation in supports of jaws.  $\times 32$ .

There is little, if anything, to separate these smaller specimens of *L. latreilli* from *L. gracilis* Ehlers\*; indeed, small specimens of *latreilli*, *gracilis*, *coccinea*, and *albifrons* converge in such a way that their sorting is a tedious business.

#### LUMBRICONEREIS COCCINEA Ren.

I doubtfully identify with this species two specimens collected, with *L. latreilli* and *albifrons*, on the shore in muddy sand, at St. Vincent and Porto Praya.

Willey† remarks that there is no definite distinction between this species and *latreilli* but the breadth of the anterior part of the body and the globular shape of the prostomium. After a careful examination of the setæ, and making drawings of a series to facilitate comparison, I have assured myself that there is no difference in this respect, making allowance for the sizes of the specimens examined. The same remark applies to the jaws.

On finding one or two specimens of *L. brevicirra* in prostomium and body form practically indistinguishable from these supposed examples of *L. coccinea*, one wonders whether a little rough handling to cause violent contraction during preservation might not be responsible for the whole difference between the two

\* Ehlers, 'Die Borstenwürmer.' McIntosh, 'British Annelids.'

† "Polychæta from the Cape of Good Hope," Trans. Linn. Soc. ix. 1903-7.

*Distribution along the body of the different kinds of Sete.*

\* indicates capillaries.

1. 2. 3 " long, medium, and short headed compounds.  
+ " crochets.

Setigerous segments	mm.																			
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.
Specimen number, † and size.																				
Suakim Harbour 1.					1				1					2	2			2	1-2	
" " 2.	2	1	1								1	1	2						2.3.	†* †*
R.S. 44 (Suez)		1			1	1			1						2	2			3	†* †*
East African	2	2	2	2	1	1	1	1	1			1.2.	1.2	1.2	3	3	3	†*	3	†*
Plymouth			2	2	2				1	1	1							2	2	2.3.
Cape Verde	3	2	2	1	1	1										1.2			2.3.	3
" " 20.	2		2			2			2										3	†*
East African		3			3		3		3		*3	†*	†*							
Wasin		3			3				*3	†*									†*	*
Cape Verde 20A.	3	3	2	2	2	2	3	3	*										†*	*

† Numbers refer to labels and slides and field note-book.

The distinction between the three lengths of the heads of compound setae is of course not definite, e.g. in S.H. 2 the heads marked 3 are longer than those marked as the same class in R.S. 44 and in smaller specimens are shorter still.

"species," striking though it is. Examination of living specimens is the only way of arriving at a decision. My own notes on the living specimens are not decisive, though they give two, not three, species collected together in St. Vincent Harbour.

The two species appear to be always found together, at the Cape or in the Adriatic as in the Cape Verde examples.

*LUMBRICONEREIS DEBILIS* Grube.

Annulata Semperiana, 1878.

The distinctive features of this species are:—

*Size* small: of my eight specimens the larger are 1 mm. in diameter, like Grube's.

*Body* form, round, with stiff body-wall and short segments anteriorly, thin body-wall and long segments posteriorly, the change taking place rather abruptly.

*Prostomium* (in spirit) oval or nearly hemispherical, as long as both buccal segments.

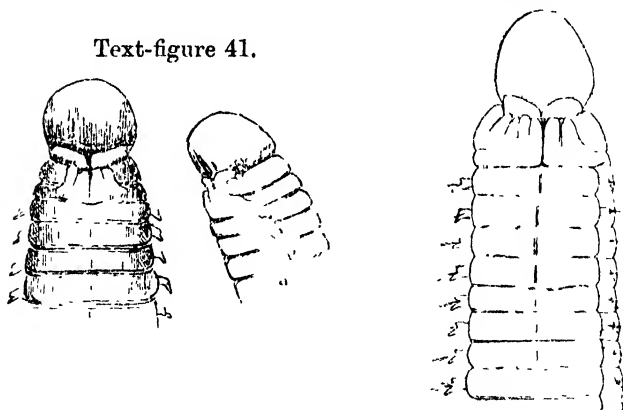
*Jaws*. Plates of second pair with strong teeth resembling those of the big dentals. Supports long. Lower jaw colourless.

*Feet* small. Hinder tip of seta-sac projects finger-fashion horizontally.

*Setæ*. No compound. Broad-ended hooks in anterior feet. Narrower—more normal in posterior feet. Capillaries broad-winged, some sharply bent.

Text-figure 42.

Text-figure 41.

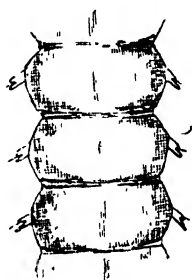


*L. debilis*.—Ventral views of specimens with oval and globular prostomium and side view of the latter. All  $\times 20$ .

The form of the body (text-figs. 41 & 42), which was noted also in the living specimens, is unusual in this though common

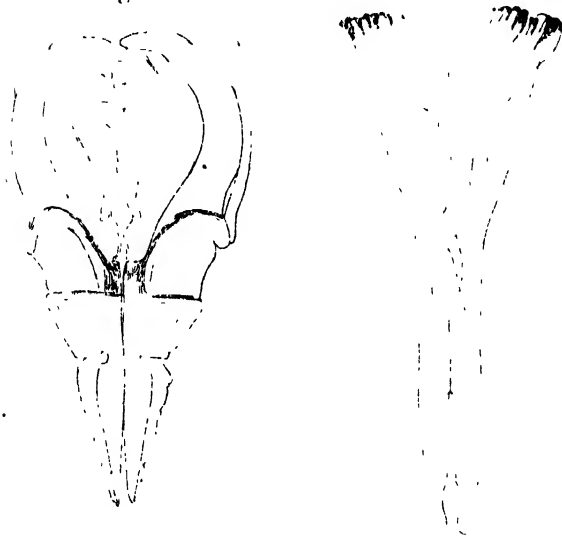
in other genera of the Eunicidæ: it is shown, *e. g.*, in *Nicidion gracilis*, figured P.Z.S. 1904, pl. xxii. of this series, and to a lesser degree in *Eunice coccinea* of pl. xx. It is common to species which live in burrows which they do not leave, and to tubicolous

Text-figure 42.

Posterior segments of *L. debilis*.  $\times 20$ .

Text-figure 46.

Text-figure 44.

Jaw apparatus, small plates of upper jaws removed.  $\times 75$ .

worms like *Diopatra*, in which the hind body has little necessity for locomotion.

The specimens here described were all obtained from Suez: (1) dredged in the bay at 4 fathoms; (2) from among coral near

shore; (3) from among a number of specimens of *Margaritifera vulgaris* from the walls of the docks. The dredged specimens were living in sponge.

Text-figure 45.



*L. debilis*.—Small plates of upper jaws from another specimen.  $\times 100$ .

Text-figure 47.



*L. debilis*. Specimen dredged at Suez.—9th foot. Winged capillaries and fine-toothed crochets,  $\times 180$ . *a*, crochet,  $\times 360$ .

The living animal is thus described :—

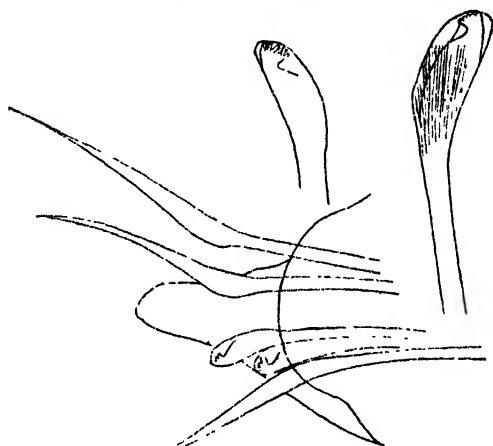
“Prostomium fairly long but very blunt, *in outline* like the bowl of a spoon. Colour pinkish, but posteriorly cream-yellow

(in this specimen *i. e.*) with sexual products, and soft like a nemertine. There is no pigment but a little yellow-brown on the prostomium. Segments in extension distinctly long and feet very small."

In spirit the body is cylindrical and of nearly the same breadth throughout, but rather broader from the 15th to 20th segments, and there is a little flattening of the ventral surface in a few anterior segments.

Anterior segments are now rather short, generally about 6 times as broad as long, in two specimens about 4 times, in one only 3 times. The change of body-form is somewhat abrupt and varies in its position, the segments at which the change occurs being, *e. g.* 25. 44. 25. 60. 70. 75; but, of course, it is not

Text-figure 48.



*L. debilis*. Specimen among coral, Suez.—10th foot. Wings of capillaries not distinct, crochets broad with distinct teeth.

possible to be exact. Behind these points the segments are about twice as broad as long (text-fig. 42).

The prostomium is oval, "*semi-ovalis paulo longior quam latus*" expresses the usual proportions exactly, but, except in one specimen, the end is rounder than in Grube's specimen, and in another it is practically globular. (Compare text-figures 41 & 43.)

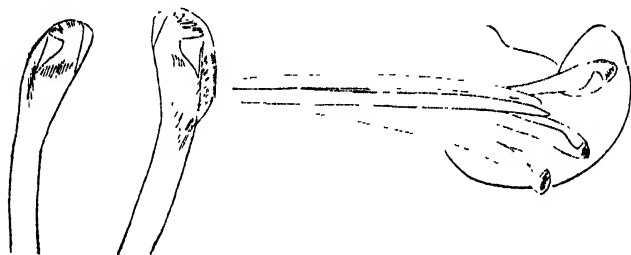
The jaws (text-fig. 44) are light brown, resembling generally those of small specimens of *L. latreilli*, but are at once distinguished by the longer supports, and the second joint in these, which has not been observed elsewhere except in *L. floridana* Ehlers. This is conspicuous in three of my six specimens mounted in balsam, clearly present in a fourth, and hardly to be



made out in the remaining two. The central parts of the supports are densely black, the lateral brown, these and some narrow bands of the pincers and parts of the accessory plates being the only black parts of the apparatus. The long lateral accessories are strong and black, and joined to the angles of the pincers. The teeth of the second pair of toothed plates (text-fig. 45) make a decided difference from Grube's description, which reads "3-ii et 4-tii angustæ, apice simplici." In view of the purely diagrammatic nature of all Grube's sketches of the dental apparatus of Eunicidæ (he gives no figure for this species) and the difficulty one sometimes has in getting these small plates into a position in which their teeth are visible, I think it likely that Grube's statement is due to an oversight. In my specimens I find the two teeth of the 2nd pair, like the single one of the anterior pair, conspicuously broad and blunt, recalling those of the big dental plates.

The lower jaw (text-fig. 46) is delicate and colourless, save for

Text-figure 49.



*L. debilis*.—Hinder (80th) foot and its setæ,  $\times 150$ .

To left: Extreme forms of the crochets,  $\times 300$ .

some black specks at the anterior lateral angles. The incurving of the posterior roots, the central ridge, and the thin brown inverted V-shaped lines are characteristic, but the latter are not present in most specimens. Text-fig. 46 was drawn from one of the largest, and shows more colour than do most.

The feet are small, posteriorly becoming very small, as is usual when the hind body is of this character.

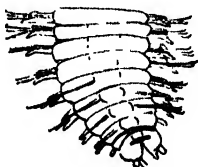
The setæ are distinctive in that hooked simple setæ (as noted above there are no compound setæ) occur in the anterior segments, where they are broad (text-figs. 47 & 48). In the hind body (text-fig. 49) they are more slender, *i. e.* of more usual form. Both these and the capillaries are broadly winged and of a yellow colour. Variations occur in the same foot and different regions, which are illustrated in the figures.

The capillaries soon disappear and in the greater part of the body (all but the anterior segments) the feet bear three unjointed hooks only.

The sketch of the anal segments (text-fig. 50) shows a local lengthening of the feet and shortening of the segments, with four small anal cirri. In other specimens this prominence of the last feet and their setæ is less marked. In the rest of the body the slight projection of the setæ is characteristic.

A specimen dredged in  $4\frac{1}{2}$  fathoms in Suez Bay is remarkable for the long and very slender capillaries of the region about the 15th to 30th feet, which are so long as to be conspicuous when the worm is examined under a lens. These are shown in text-

Text-figure 50.



Anal segments.  $\times 20$ .

figs. 51 & 52 of the 15th and 28th feet; the latter is apparently close to the point at which the capillaries disappear altogether, but no more of the hind body was obtained. The other capillaries, as shown in text-fig. 47 of the 9th foot, are normal in shape; but whereas in other specimens the distinction between shaft and

Text-figure 51.



Specimen with prominent capillaries. 15th foot.  $\times 80$ .

wing is obscure it is here clear, and there is some striation. The crochets are somewhat narrower.

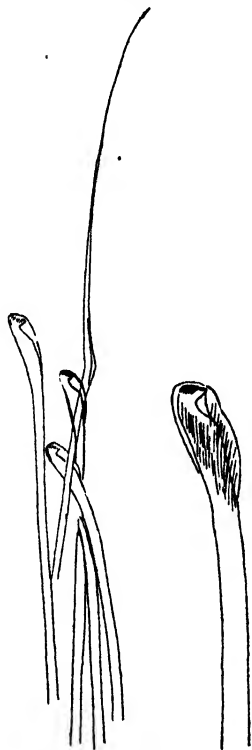
In other respects, *e. g.* pro- and peristomia and jaws, the specimen was normal (text-fig. 43 of the anterior end is from this specimen), and there is no doubt of its being of this species.

A similar extension of the capillaries in the corresponding region of the body was noted in certain specimens of *L. latreilli* from the Cape Verde Islands. It may be connected with the

quieter habitat below tide-level, but, as shown by the differences in the other setæ, it is clearly constitutional, not merely a mechanical result of easier conditions.

Work done since Grube's time shows that there is nothing remarkable in the extension of a species from the Philippines to the Red Sea, but its absence from the Maldivan and East African collections is perhaps notable.

Text-figure 52.



Same specimen, 28th foot,  $\times 90$ . Crochet,  $\times 180$ .

The parallelism between this species and *L. albifrons* of the Atlantic is but one case of a series which might be made out, and is obviously connected with similarity of habitat.

This species somewhat resembles *L. cingulata* Treadwell\* (the name *cingulata* is preoccupied by a species described by Ehlers in the Magelhaenische Sammelreise), but differs in the *apparently* flatter body, elongation of the prostomium, and shortness of the

\* 'West Indian Leodiciæ.'

jaw supports. One regrets that Treadwell's beautiful figures of the living animals are not accompanied by outlines of the same parts after preservation, as most systematists have to be content with spirit specimens. For instance, in this case it is possible that a spirit specimen might closely resemble *debilis* in the proportions of pro- and peristomium, and the curious and distinctive tubercles upon them may be no longer visible.

It is also possibly identical with the species *L. cavifrons* Gr. 1866=*capensis*=*dubeni*, but, owing to the brevity of descriptions given and the omission of mention of the striking form of the body, certainty is not possible. Fauvel mentions that his *L. cavifrons* from Mozambique and Madagascar is very near to *L. impatientis*, from which my species is quite distinct.

*LUMBRICONEREIS MANDO* \*, sp. n.

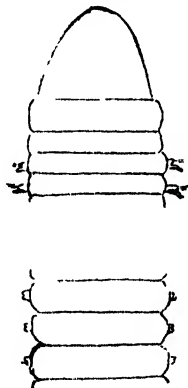
The species is distinguished by the extraordinary length and slenderness of the shafts of the mandible.

The maxillary jaw-plates are also distinctive.

Prostomium broad and flat, approximately an equilateral triangle.

Segments short ; feet small, becoming smaller posteriorly.

Text-figure 53.



*L. mando*, sp. n. -Above, head and anterior segments ; below, segments about 40th with reduced feet.  $\times 10$ .

No compound setæ ; capillaries and hooded crochets of usual type.

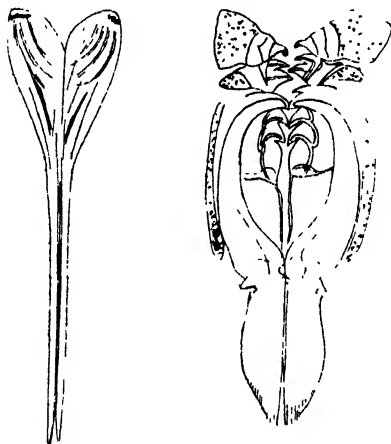
One specimen was dredged in  $4\frac{1}{2}$  fathoms in Suez Bay, bottom sandy mud. It is incomplete, and now softened, only the head and 50 segments being present. The body is round, very little

\* *Mando*, Latin=*glutton*, in reference to the special development of the jaws, especially mandibles.

flattened ventrally, and of uniform thickness from the peristomium to the end of the fragment, 1.7 mm. thick and 25 mm. long. The segments thus average a little under half a mm. in length; i. e. varying between one-third and a quarter of their breadth. Prostomium the shape of an equilateral triangle and, as shown in text-fig. 53, of fair size in proportion to the body dimensions. No sense organs are visible. The peristomium has the usual structure.

Text-fig. 54 shows the peculiarities of the jaw apparatus, the most striking of which is the extreme length and slenderness of the lower jaw, these characters being more marked than in *L. bifilaris* Ehlers\*, which is the nearest approach in species hitherto described, though quite different otherwise.

Text-figure 54.



*L. mando*, sp. n.—Upper and lower jaws.  $\times 30$ .

The cutting-edges are smooth and very oblique, meeting in a deep V. The whole is nearly colourless save for the light brown lines indicated.

The maxillæ are dark brown, not black, in spite of their large size, and are peculiar in that the dental plates extend only about half-way down the forceps. The articulation of the bases of the forceps to each other and to the supports and the two spurs pointing laterally are distinctive. Other details may be obtained from the figure.

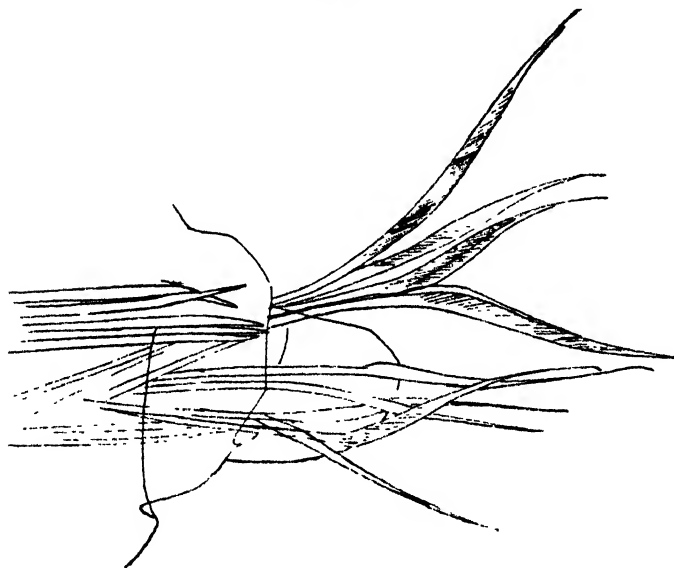
\* Ehlers, *Mag. u. Chil. Strandes*, Taf. xviii. fig. 9 a. Chamberlin (*l. c.*) identifies with this species a number of specimens from Mexico and Chile of which the mandibles are conspicuously short for the breadth of the end plates. As he gives no intermediates connecting this form with that of the type, it is scarcely possible to regard the identification as certain.

The feet are small, and are best developed in the first few segments, becoming decidedly smaller posteriorly, the reverse of the usual rule, and the posterior lip of the seta-sac projects very little in these hinder feet.

Setæ all simple in anterior feet.

The 10th foot is figured (text-fig. 55), and shows 9 capillaries of which the dorsal bundle of four are large and project well, the

Text-figure 55.



10th foot.  $\times 200$ .

ventral being smaller. Slight variations in shape and structure are to be noted. The striation is finer than represented, but it evidently goes deep, as there is a marked tendency for the setæ to break along the striæ, as indicated in the dorsal example. Wings are narrow or not present. All have slender tips often tenuous. This foot contains five curved and more or less slenderly pointed aciculæ; the 20th has seven capillaries and four aciculæ; the 30th two each of capillaries, aciculæ, and hooded crochets, also a bundle of five slender colourless and very flexible aciculæ apparently belonging to a (now invisible) dorsal cirrus. These are bent back upon themselves without breaking as in some other species. In foot 50 and thereabouts there are no capillaries, four (or three) crochets, and the usual five slender bent cirrus aciculæ.

The crochets are all alike, and as shown in text-fig. 56. The

upper teeth are distinctly swollen distally. The colour of all setæ is yellowish, the crochets being the darkest, rather dark straw-colour.

Text-figure 56.



*L. mando*.—Crochet.  $\times 375$ .

# **LUMBRICONEREIS BREVICIRRA Schm.**

## *Short description.*

Body of usual proportions, not much narrowed to head.

Feet in forebody small, over posterior three-quarters fairly long.

Prostomium bluntly conical, sometimes triangular.

Jaws of normal pattern, mandibles with deep brown crescentic lines in anterior cutting-plates, rest white.

Setæ consist of crochets and capillaries only. The former are found in the first feet as well as the rest of the body. All are fairly broad-ended anteriorly with a wing extending down the shaft; posteriorly the heads and wings are short.

Capillaries die out about the 35th foot.

In spite of my specimens being all from the Atlantic—abundant in the Cape Verde Islands and absent from the Indian Ocean and Red Sea,—I am inclined to identify them with *L. brevicirra* Schm. recorded from South Australia\*, New Zealand†, and Fiji‡. One of the principal differences is in the mandibles, which in Ehlers' figure are of remarkable breadth, diverging instead of tapering posteriorly. Augener and Treadwell, however, agree that Ehlers probably had in hand an abnormal specimen. It is curious that a parallel, but further exaggerated, difference exists between the descriptions of the nearly related *L. impatiens* by De St. Joseph and McIntosh, which inclines one to think

\* Schmarda and Augener.

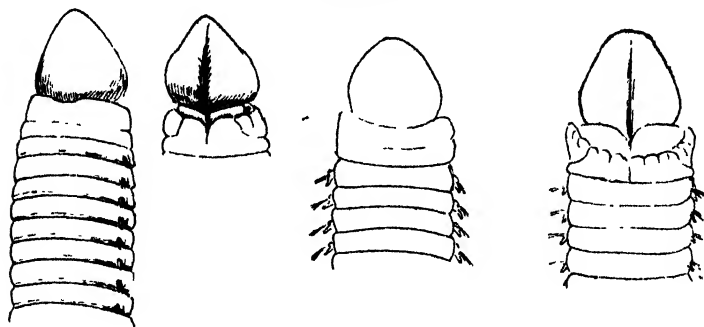
† Ehlers.

‡ Treadwell.

that there is more than chance abnormalities underlying the phenomena.

The standard description of *L. brevicirra* Schm. is given by

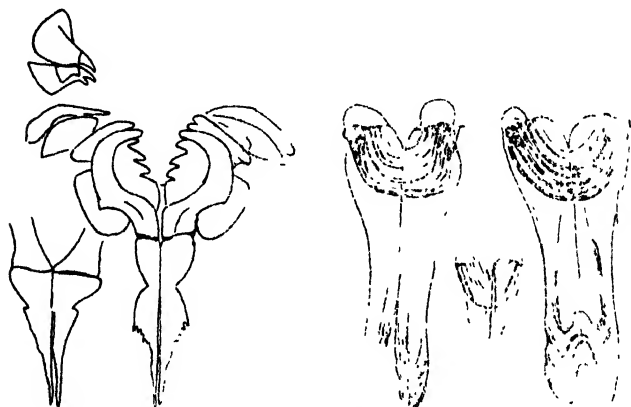
Text-figure 57.



*L. brevicirra*.—Dorsal and ventral views of two specimens from Sal showing variations in pro- and peristomia, etc.  $\times 10$ .

Ehlers in his "Neuseelandische Anneliden,"\* who, however, besides the rather doubtful figure of the mandibles, does not figure the characteristic anterior crochets, and leaves it doubtful whether the narrow crochets found in *L. impatiens* also occur

Text-figure 58.



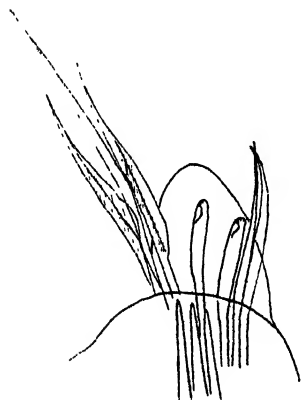
Jaw apparatus of several specimens. All  $\times 30$ .

here. The crochet he figures is seen from the edge and shows neither its proportions nor details of hooks, etc. The micrometer measurements of the crochets' heads, given in his text, agree

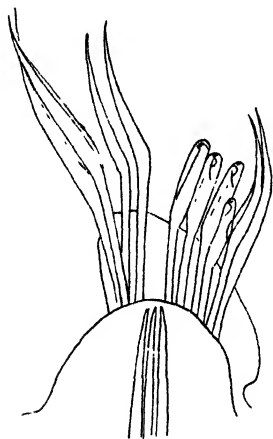
\* Abh. K. Ges. Göttingen, iii. 1904.



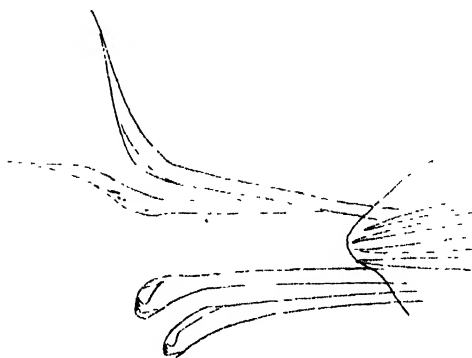
Text-figure 59.



Text-figure 60.



Text-figure 61.



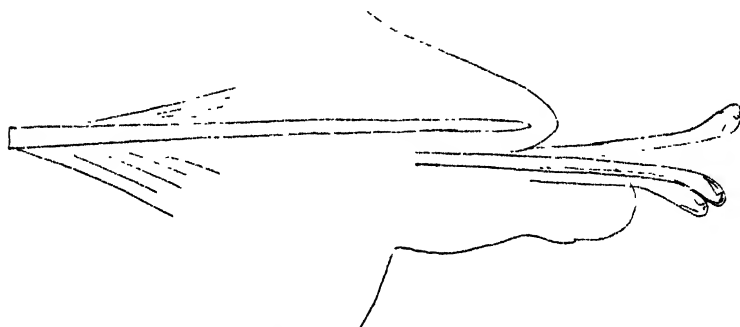
*L. brevicirra*.—Feet 5, 12, and 27. All  $\times 120$ .

fairly with the specimens from the Cape Verde Islands. Under these circumstances the only plan is to describe these specimens fully and leave subsequent work to decide whether they are really *L. brevicirra*—or possibly *L. inpatiens*, and if the former, confirm the unexpected distribution of the species thus indicated.

Schmarda's and Ehlers's specimens were all found in sand, on which Ehlers remarks: "This agreement in the nature of the habitat in both localities shows, perhaps, a peculiarity in the life-conditions of the species." Treadwell found his in sand in a reef pool (presumably a clean coarse sand) and also in mud. In the Cape Verde Islands it occurred in muddy sand in St. Vincent Harbour and Porto Praya and in clean white sand in the Island of Sal. In the former cases other species (*coccinea*, *latreilli*, and *albifrons*) were found at the same time, whereas at Sal all the Lumbriconereidæ found were of this species alone.

The prostomium (text-fig. 57, four sketches) is conical, but

Text-figure 62.



One of the hind feet.  $\times 75$ .

shorter than in *L. latreilli*. There is considerable variation as shown in the sketches given, which do not include the extremes. One specimen had a prostomium as long as that of *L. latreilli*, and in another, which had contracted badly in killing so that the anterior segments were extremely narrow and the jaws practically protruded, the prostomium is a flattened sharply pointed equilateral triangle. It is sometimes almost globular, except for being pointed in front. I have not seen the nuchal organs sketched by Ehlers. A characteristic of *L. brevicirra* is the faintness of the dividing line between the two rings of the peristomium, a feature found in the majority of my specimens. Generally the anterior ring can be made out to be twice as long as the posterior.

Treadwell finds more plications of the oral process of the second ring than the very simple arrangement shown by Ehlers, as I do in certain specimens. The body-form resembles that of

*L. latreilli* and other species, but the most anterior segments are little narrower than the maximum breadth. The segments are of the usual proportions, becoming longer posteriorly in the usual way. The feet, however, are very small in anterior segments and all through the first quarter, but become prominent in the rest of the body, *i. e.*, the posterior three-quarters. They are all of the usual structure with horizontally projecting lip process.

The characteristic features of the jaw apparatus are :—

- (1) The long narrow posterior roots of the supports of the upper jaw, which are always found, though there are large variations in shape of supports.
- (2) The shortness and curvature of the pincers.
- (3) Prominence of the ridge at the head of the big dentals.
- (4) The dense black narrow concentric lines of the mandibular end plates and the colourless but wrinkled posterior roots.

Text-figure 63.



*L. brevicirra*.—Crochet setæ from 5th, 10th, 12th (one example), and 27th feet.  $\times 336$ .

Capillary of the dorsal bundle of 10th foot.  $\times 170$ .

These features are shown in text-fig. 58, in which the extreme forms of the supports are given. The upper toothed plates are drawn from another specimen in which they had been brought into view by pressure.

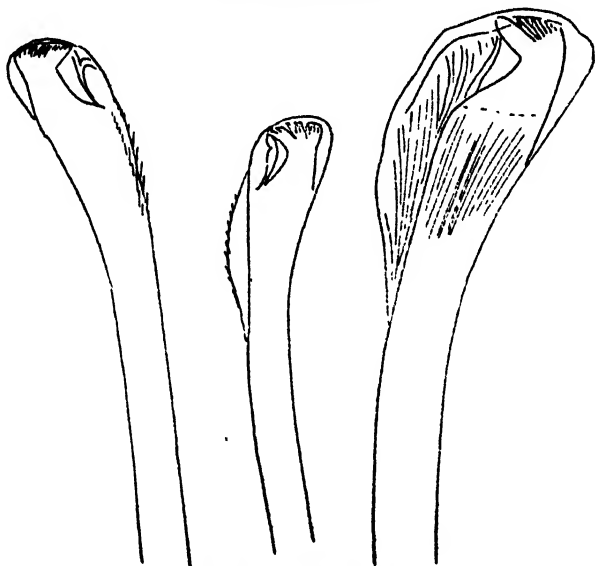
The three figures of the mandible show the varying development of the dark crescentic lines, etc. The beginnings of this feature are visible in the very small specimen in the middle (all figures are to same scale). In some specimens these lines are principally developed in a rather narrow band along the circumference

of the semicircle. The wrinkling of the calcareous roots naturally varies with age: in the figure to the right there is some approach, in this feature and in the expansion laterally of the posterior roots, to the figure given by Ehlers.

The setæ are fully described by the series of outlines given (text-figs. 59 to 64). The capillaries are slightly yellowish, the broad-ended crochets and aciculæ which accompany them colourless. In posterior feet the crochets become quite yellow and the single acicula is tinged light brown.

It will be noted that the crochets of anterior feet are not much narrower than those of the posterior part of the

Text-figure 64.



Crochets of hinder feet.  $\times 400$ .

fore-body (text-fig. 63), thus distinguishing the species from *L. impatiens*. Nor do I find the intermediates between capillaries and crochets which form so interesting a feature of the latter species \* and *L. hibernica*. Of the figures given no. 64 a, which shows a crochet from a hinder foot, agrees fairly well with Ehlers' figure of one from the 136th foot. The upper teeth have now become so extraordinarily fine as to be hardly visible until a  $\frac{1}{12}$ -inch objective is used, whereas in anterior feet, in spite of variations, they are generally distinct. Under a  $\frac{1}{8}$ -objective some of

\* See McIntosh, Brit. Ann. pl. lxxxi, 4-4 d.

my specimens show the peculiar arrangement given by Fnuvel's figures for *L. impatiens* from Obock, French Somaliland, but the  $\frac{1}{2}$  inch objective resolved them into the more normal form figured.

The capillary setæ are shown in text-fig. 63 and in figures of the feet. They are rather straight and short and offer no peculiarities. In the 5th foot it will be noted that only two of these setæ have appreciable wings and striations. The dorsal capillary from the 10th foot in text-fig. 63 is drawn to only half the scale of the crochets.

*LUMBRICONEREIS ALBIFRONS*, n. nom.

*L. cavifrons* McIntosh, Marine Investigations of the Cape of Good Hope, 1903, p. 50.

A small species with short body of nearly full diameter to anterior end and somewhat long segments posteriorly.

Prostomium nearly globular, generally smooth above and below.

Jaw apparatus remarkable in that max. II is more or less crescentic and bears three or four teeth instead of the two or one usually carried, max. III having two each. Mandibles delicate and colourless when not rudimentary or absent.

Compound setæ and unjointed hooks in anterior feet. The former have very short heads more or less imperfectly separated from their shafts.

Most specimens are small, the majority being about half a millimetre wide, but a few larger up to 1.3 mm. in width without the feet occur.

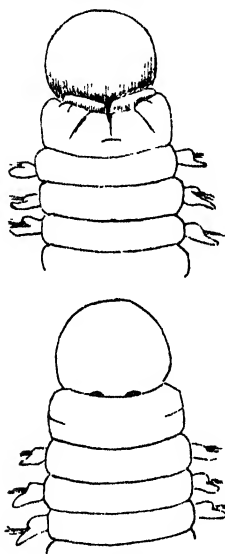
A series of specimens observed in life were easily picked out among other small polychæta, including small specimens of *L. latreilli* collected at the same time, by their conspicuous white prostomia. These were in life longer than broad; in one specimen it was noted that the prostomium was rather broader than the body, bluntly rounded in front. The body was coloured a light yellow-brown with a thin chocolate line across each segment; in anterior segments another very thin line before and behind this. The peristomium has three lines, all darker than those on the body. The segments appeared thickened where the very small parapodia were attached.

The form of the body recalls *L. debilis* in that the segments are longer in the hind-body, but while in both the proportion of breadth to length in anterior segments is from 4 to 6, it is only 3 posteriorly in this species against 2 in the preceding. There is a slight flattening ventrally through all the fore-body, not for a few segments only, but it is quite round behind. It tapers gradually to the tail, but while in one

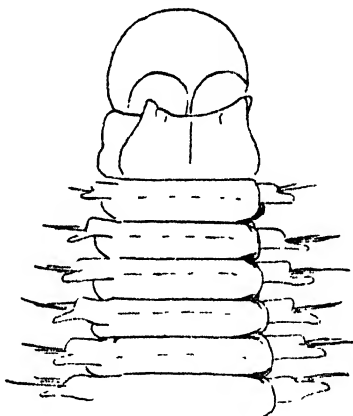
specimen this tapered portion is a third of the body-length, in another it is scarcely a tenth. Development of sexual products might account for this difference. Anteriorly the body is very slightly narrowed. There are four tiny anal cirri, with swollen bases as usual.

The prostomium, as shown in text-figs. 65 and 66, is practically globular, and generally without grooves on either surface. The exposure of the "mundpolster" and furrowing of the lower margin of the mouth vary, so that the appearance of a ventral view of the head is not constant. The division of the peristo-

Text-figure 65.



Text-figure 66.



*J. albifrons*.—Dorsal and two ventral views of anterior ends.

Fig. 65  $\times$  30. Fig. 66  $\times$  40.

mium into two rings can hardly be made out, but at times a light mark appears laterally indicating an anterior ring somewhat broader than the next. Succeeding setigerous segments are all alike as shown in the figures, until they lengthen posteriorly.

The upper jaws (text-fig. 67) are sufficiently described by the sketch, attention being drawn to the crescentic maxillæ II bearing four teeth. It is unfortunate from the systematist's point of view that this, the most striking peculiarity of the species, unique in the genus, should be one which is often difficult to make out. It is of interest morphologically as a connecting link with other Eunicidæ.

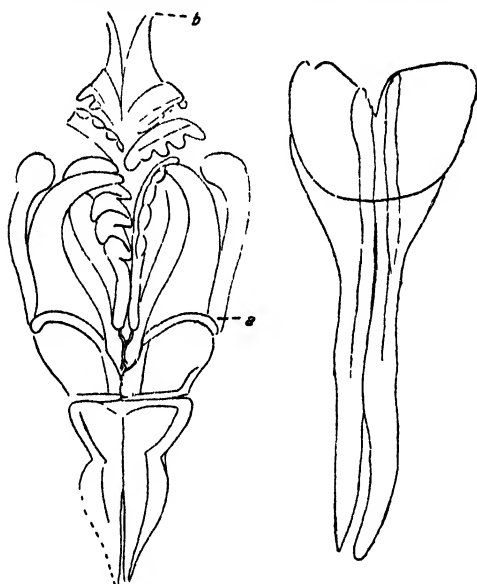
The numbers of teeth vary in the usual way, as shown by the formulæ:

2—2.	2—2.	2—?
4—3.	3—?4.	?—3.
4—5.	5—5.	?5—6.

The number of interrogation marks indicates the difficulty of examining this minute apparatus, but it is in all cases clear that more than two teeth occur on the second pair of plates and more than one on the third (*i. e.* anterior).

Text-figure 67.

Text-figure 68.



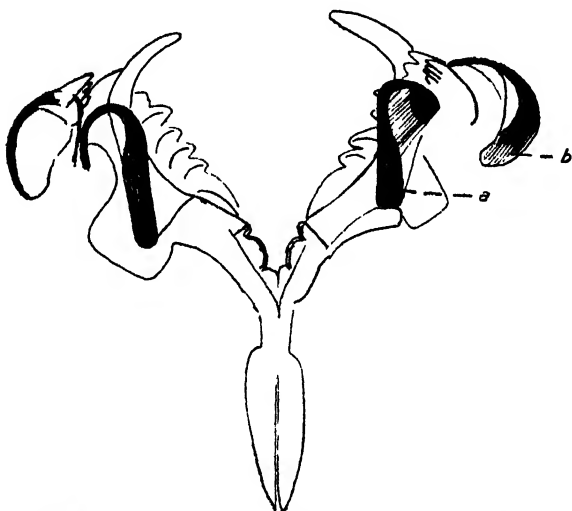
*L. albifrons*.—Upper and lower jaws of different specimens.  $\times 10$ .  
The points *a* & *b* correspond to those marked in fig. 69.

Text-fig. 69 illustrates the positions of the plates when protrusion is beginning. The bending of the black accessories to the first plates and pincers is remarkable, the points *a* and *b* indicating the positions of the same parts at rest and under extension. The connections between the various plates, as shown when under action as here, are complicated, and the method of extension would be an interesting subject for investigation. In this figure plates II and III are both in one plane vertical to the paper, so that the teeth they bear cannot be clearly shown.

The mandibles were not found by McIntosh in the specimens he dissected, but out of seven or eight of mine, I found it in three (text-fig. 68). It is of great delicacy and quite colourless, in one case a mere ghost of a mandible as it were. It may be fairly concluded that in many it is in fact absent.

The feet (text-figs. 70 & 71) are small and of the usual pattern, *i.e.*, a rounded anterior lobe, the posterior lobe having a finger-shaped process which projects horizontally. In the hind-body the feet are smaller, but of the same pattern. The setæ (text-fig. 72) are of the three kinds described by McIntosh, but the heads of the compound setæ are generally even shorter in my specimens. The broad uncinatæ setæ become more slender in their head ends, *i.e.*, of more normal pattern, in the hind-body.

Text-figure 69.



Upper plates in course of protrusion, showing bending of accessory bands.  
a, b correspond to points so marked in fig. 67.  $\times 130$ .

There are two distinctive features of these hooked setæ :—

- (1) Compound and simple hooks may both occur in the fore-body.
- (2) The jointing of the compound setæ is incomplete.

Text-fig. 72 shows stages in the formation of a compound from a simple crochet. In the most advanced stage the hood remains entire, not even notched, between the head and the shaft. While the lower part of the joint is perfect the upper may be distinct as regards the shaft, but indefinite in the end piece. In other cases the division between shaft and end piece is a mere crack which does not extend quite to either end of the division. These

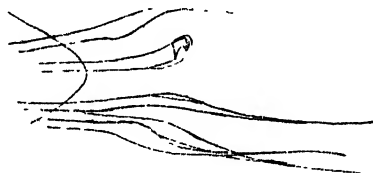


short-headed setæ are not, however, an infantile feature in *this species*, as they occur in the largest specimen of the considerable number obtained, which is of a size at which long-headed compounds would be abundantly developed in *L. latreilli* or *L. coccinea*. They do, however, like the crescentic max. ll., indicate that the species itself is in some ways primitive. As shown in figures of feet these setæ occur in small numbers, one or two to a foot.

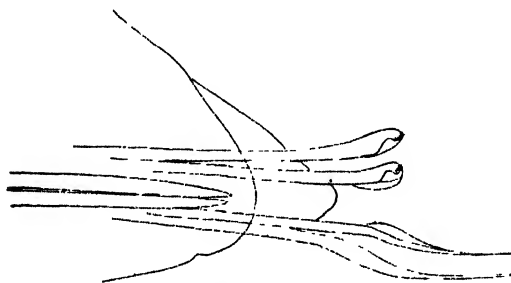
The capillary setæ have broad heads, but show the usual variations in this respect.

In the "Marine Annelids of the Cape of Good Hope" McIntosh gives *L. carifrons* Gr., and *L. gracilis* as synonyms. Fauvel (*l. c.*)

Text-figure 70.



Text-figure 71.



*L. albifrons*.—Feet 20 and 40.  $\times 150$ .

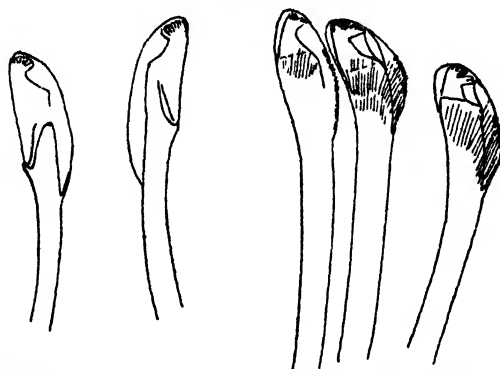
remarks that the species from the Cape is not *carifrons* Grube as it has compound setæ. It has been suggested above that *L. gracilis* may be the young form of *L. latreilli*, from which this species is readily distinguished by (1) body-form and small feet; (2) globular prostomium; (3) possession of short-headed setæ and unjointed hooks in anterior feet in specimens 1.5 mm. in diameter, a size at which in either *L. latreilli* or *L. coccinea* long-headed compounds would be conspicuous; (4) the anterior jaw-plates with 4 and 2 teeth respectively.

This species shows strong resemblances to *L. sphærocephala* Schm. as redescribed by Ehlers\*. The prostomium is, however,

\* "Neuseeländische Anneliden," Abh. Kön. Ges. Göttingen, 1904.

longer in the latter\*, and though the form of the body is very similar anteriorly the segments become shorter, more strongly marked, and their feet apparently more prominent posteriorly. A great point of similarity is the short-headed compound setæ in which the wing is continuous from head to shaft, but the capillaries and crochets differ in detail—resembling rather those of *L. debilis*. The upper jaw apparatus has similar long pointed supports, but the broad angles of the pincers connecting with the long accessory plates at their sides are wanting, and above all

Text-figure 72.



*L. albifrons*.—Setæ. On left, compounds from feet 10 and 11 with more or less separation between heads and shafts; middle, pair of crochets from 4th foot; on right, from 20th foot. All  $\times 335$ .

*L. sphaerocephala* has the usual upper plates with 2 and 1 teeth on each side.

As would be expected from the body-form, the species was found inhabiting crevices in Lithothamnina, etc., (1) dredged from 3 fathoms in St. Vincent Harbour, (2) a few on shore in the same bay, and (3) at Porto Praya, Santiago, and half-a-dozen from "washings" nos. 7 and 12. It was not found in the Red Sea or Indian Ocean, where *L. debilis* seems to be a parallel form.

#### The Genera DRILONEREIS and ARABELLA.

In 1904 the genera in which the maxillary supports are long thread-like processes were in such confusion that one despaired of making order without the re-examination of a number of old collections. I now follow Treadwell†, who, having a number of species of both genera in hand, simply divides the Lumbriconereidæ into four main genera, *Lumbriconereis*, *Drilonereis*, *Arabella*, and *Cenone* (*Aglaurides*), the second and third genera

\* Treadwell's specimens from Fiji and Samoa also had shorter prostomia.

† 'West Indian Leodidæ,' 1921, p. 94.

including *Aracoda*, *Laranda*, *Maclovia*, etc., the species of which fall into sometimes one, sometimes the other, of the two genera retained.

Chamberlin\*, in 1919; revived the old genera and added several new ones, of which *Cenothrix* is an *Arabella* distinguished only by the possession of guards on the acicular setæ†, and *Cenogenus*, an aberrant type with toothless maxillary plates and degenerate supports, while in *Biborin* the maxillæ are absent altogether. These and other distinct genera, such as *Notocirrus* and *Ninoe*, are not represented in these collections.

The two genera are readily distinguished by their jaw apparatus, no species not readily falling into one or the other having yet been discovered. Briefly, *Drilonereis* has large forceps and small toothed plates, of which only the proximal is of any size, the distal often mere hooks, while in *Arabella* the proximal plates are not forceps and not very greatly larger than the series anterior to them, which gradually decrease in size, only the anterior of all being simple hooks. However, the species may be arranged in a regular series, from the extreme *Drilonereis* type in which the large forceps are toothless at the base, the other plates of insignificant size and all the anterior ones simple hooks, to species which approach *Arabella* in having toothed bases to the forceps, the other plates of considerable size, and even the fourth pair have two or three teeth. There may even be a fifth pair of hooks; Treadwell found an extra hook in one specimen of *D. brunnea*, and in *D. (Aracoda) debilis* Ehl. the extra pair seems to be normal.

The mandibles are usually absent in *Drilonereis*, well developed in *Arabella*, but they are occasionally present, in a distinct though rudimentary form, as an individual variation in most species of *Drilonereis*‡.

In the same way the apparatus in *Arabella* is, in its main lines, hardly distinguishable from that of symmetrical specimens of *Ænone*, and the first maxillæ in *Arabella* have been found to make a beginning of the asymmetry characteristic of that genus.

*Lysarete* is a remarkable intermediate form connecting these genera, through *Ænone*, with *Lunbriconereis* and the other Eunicidæ. Practically *Lysarete* is an *Ænone* in which the jaws,

\* Mem. Mus. Comp. Zool. Harvard, xlviii. 1919, p. 325.

† The multiplication of genera on such small points is to be deprecated as in no way tending to order or to facilitate future work. Compare the same author's new genus "*Aphelothrix*" for the reception of the well-known *Marphysa mossambica* and his new name "*Pterothrix*" for *Notocirrus scoticus* McL., given on purely literary and circumstantial evidence, to the unnecessary confusion of the literature.

‡ It has been discussed whether the more or less triangular third support of the jaw apparatus in *Drilonereis* represents rudimentary mandibles. As in those specimens of *D. major* in which the rudiments of mandibles existed also showed the third support, as was the case in some of Fauvel's specimens, it is clear that there is no connection between the two structures. When present the mandibular rudiments are situated far anterior to the junction of the supports, and come in front of the other jaw-plates. Compare also the genus *Arabella*, in which the lower jaws are well developed in all species, while yet the third support is present and sometimes almost as well developed as the usual paired ones.

by shortening of the supports and modification of the first plates into pincers resembling the antlers of a stag, approach the highly specialised arrangement common to the genera *Eunice*, *Lumbriconereis*, *Onuphis*, etc.

#### Genus DRILONEREIS.

Species of this genus are not found in many collections. Even the 'Challenger' has only one (*D. longa*), while Treadwell, by concentrating upon the Eunicidae alone, obtained no fewer than eight species (six from the West Indies and two from Fiji and Samoa), of which seven were new. Moore has *D. nuda* from California\*, Ehlers *D. debilis* from Florida and *D. annulata* from East Africa.

We thus have thirteen species, of which only three are from the Old World, and of these three Fauvel believes two, *D. longa* and *D. filum*, and perhaps *D. annulata*, to be synonymous; while Treadwell, after examination of American specimens, doubts the identity of McIntosh's *D. longa*† with the species, also American, described by Webster. The present collections add two new species to the Old World fauna.

It seems remarkable that while species of *Drilonereis* were collected at Suez, Suakin, and Zanzibar, the only species, *D. filum*, which Fauvel records from similar habitats in this region, was not found.

The examination of these small jaw-plates needs great care. Even in such large specimens as my *D. major* certainty was frequently not possible without dissection and separation of the upper plates from the forceps. The least obliquity of the plates means the disappearance from view of one or more teeth and the alteration of the apparent shape of the plate itself. The specimens were therefore examined: (1) *in situ*, (2) after removal, (3) mounted and dissected.

The method by which the pincers are connected to the supports seems to be a feature of possibly systematic importance. It has the advantage of being easily observed as a rule.

#### DRILONEREIS MAJOR, sp. n.

*Body*, in spirit, up to 3.5 mm. wide and 43 cm. long. One specimen when alive was 3 mm. wide by 65 cm. long (26 inches  $\times \frac{1}{10}$  inch). This is an enormous size for the genus.

*Prostomium* flat and hollowed ventrally as usual in the genus. Almost semicircular in outline, peculiarly ridged on dorsal surface. No sense organs of any kind.

*Peristomium* in two nearly equal segments, forming ventrally a

\* The same author describes a *Laranda robusta* from Japan which appears to be a *Drilonereis*, but as the jaws are not even mentioned and nothing is figured but two setae, the reference is best ignored.

† Var. *elisabethæ* in 'British Annelids.'

straight unwrinkled margin to the large mouth. It may or may not be continuous with the prostomium dorsally.

*Parapodia* invisible anteriorly, appear outside body as very small projections about segment 15; they gradually become more prominent, and in the posterior region each equals one-third the breadth of the body, the long posterior lobe of the seta-sac being included in the length of the foot.

*Setae* all simple as usual in the genus, but divisible into six kinds. The long capillaries are slender, but slightly bent and not distinctly bordered.

*Jaws* of normal type. No teeth on bases of pincers. Accessory plate of supports triangular, generally about equilateral. Rudiments of mandibles usually absent, sometimes conspicuous. Formula of teeth about

$$\begin{array}{r} 1+1-1. \\ 1+4-1+1+? \\ 5-6. \\ 0-0. \end{array}$$

The collection contains four specimens collected by digging in sand among a small species of "seagrass" (*Zostera* or *Cymodocea*) at low tide at Suez on the mud-flats, and a fine series of ten specimens collected by J. Gordon Logan, Esq., in front of the Hotel Sinai, from a tidal basin which is now filled in. The two localities are two or three miles apart. Also one small specimen from Zanzibar.

Through Mr. Logan's kindness I thus have the material for an examination of the variability of the jaw apparatus, which, after the discovery of the striking peculiarities in *Enone* and Fauvel's statements of the great range in *D. filum*, promised to be interesting.

But for trifling differences in the numbers of the teeth I find remarkably little variation, and am therefore inclined to doubt Fauvel's statement that *D. filum* Clp. and *D. longa* Webster (and McIntosh) are synonymous. The rudiments of the lower (mandibular) plates are sometimes conspicuous but generally quite absent, which seems to be the case in several species. Their presence or absence cannot be reckoned among specific characters.

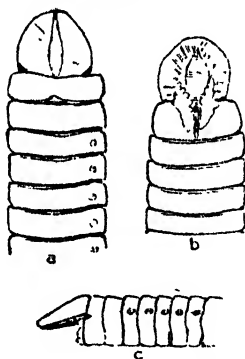
The body is, as usual in the genus, of nearly uniform thickness. It is stoutest for the next three or four inches or so after the 15th segment, after which it becomes slightly more slender and flatter, tapering very gradually towards the tail; at the tail end itself it tapers rapidly, unless, as is frequently the case, it is undergoing regeneration. Before the 15th segment, *i. e.* in the region containing the jaw apparatus, the body narrows to about two-thirds its maximum thickness, and is flattened ventrally, strongly arched dorsally, but this narrowing ceases six to ten segments before the head, these first segments being all of the same width.

The colour of the living animal uniformly reddish yellow in smaller specimens, chestnut-brown in larger. In fresh water and alcohol (added for narcotisation before killing) a bluish solution, like the ink of *Aplysia*, appears, as in the case of *Ænone fulgida* and *australis*, and others of this family.

The feet do not project at all for the first 6 to 16 segments, appearing as mere dimples on the surface (text-figs. 73 *a* & *c*), after which for about 20 segments more the finger-like posterior lobe alone projects. Then the foot itself appears, but is very short and stumpy for some distance, but gradually elongating until, in the posterior two-thirds of the body, it is conspicuously long. The postero-ventral lobe is now as long as the foot itself, and both together equal a third of the breadth of the body. In the short, thick anterior feet this lobe may be half as long again as the foot itself, *i. e.* its development precedes the full length (or protrusion) of the foot.

The body-wall anteriorly is remarkably tough.

Text-figure 73.



*Drilonereis major*, sp. n.

*a* & *b*, dorsal, *c*, lateral views of anterior end.  $\times 6$ .

In *a*, pro- and peristomia distinct, in *b*, dovetailed.

In *a*, radial lines faint, in *b*, distinct.

In *a* & *c*, parapodial dimples with setae broken off short.

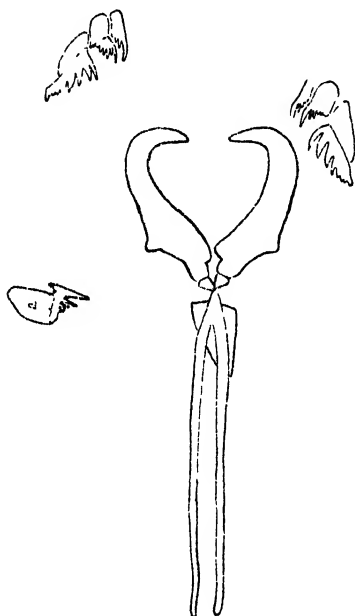
The prostomium (text-figs. 73 *a-c*) is, as usual in the genus flattened and hollowed underneath. In this species it is nearly semicircular in all cases, so that the ventral view resembles a horse's hoof without the "frog." Dorsally is a central depression and radial ridges peripherally. The latter in some examples are indistinct and might be overlooked if not already seen in other specimens.

The peristomium consists of two equal segments remarkable for their simplicity and absence of either folding or notching in connection with either sense organs or the mouth. They are almost perfectly cylindrical.

As a rule, the separation of pro- and peristomia is distinct, but specimens occur in which they are continuous dorsally or in which the prostomium seems to be dovetailed into the peristomium. In one case where pro- and peristomium were continuous, even to the extent of the continuation of the median depression of the former as a faint line upon the latter, there was still a distinction between the light colour of the pro- and the darker tint of the peristomium.

As these variations are apt to be reckoned as of specific importance, I figure examples in order that their character and extent may be appreciated (text-figs. 73 *a* & *b*).

Text-figure 74.

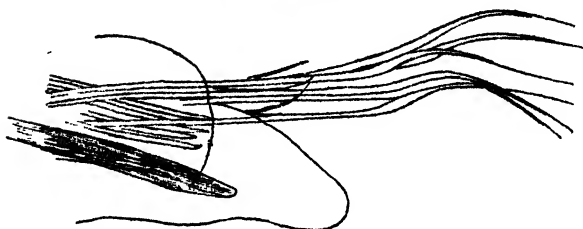


*D. major*.—Jaw apparatus, dissected.

*a*. Max. III seen at an angle causing large apparent change of shape.  $\times 23$ .

The jaw apparatus (text-fig. 74) is quite typical of those species in which the broad bases of the pincers have no teeth. They have a single knob on one side, as in *D. nuda* Moore, which resembles this species generally in the structure of its jaws, but is otherwise distinct. The following table gives the variations found in the ten specimens specially examined. As in my description of *Ænone*, the first figure in a line means one (or two) teeth enlarged to hooks, the second the number of teeth of

Text-figure 75.



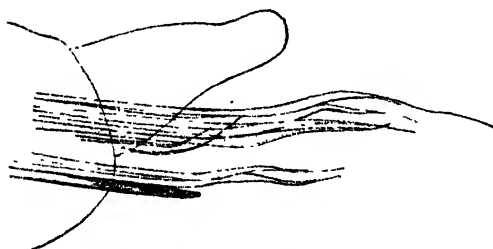
*D. major*.—An anterior foot (65th). Ventral setæ broken off short, the stumps overlying the broad acicular seta.  $\times 23$ .

Text-figure 76.



A posterior foot showing dorsal tubercle and its setæ, aciculæ and acicular seta (dotted) and capillaries.  $\times 33$ .

Text-figure 77.



Another posterior foot illustrating differences in the shapes and details of setæ. To larger scale, *i. e.*  $\times 75$ .



approximately equal size and easily counted, the third small denticulations, while the ? mark means that though denticulations exist they are too small and indistinct for certainty.

Specimens collected by C. C. in open bay :—

	Spec. 1		2		3	
IV.	1+1	?*	1+?1	1+1	1+1	1
III.	1+3	?*	1+3	1+4	1+3	1+4
II.	4	2+4	6	2+4	6	2+5
I.	The forceps show no definite variations, but shape varies with degree of separation.					

\* Not clearly seen.

Collected by J. G. Logan in tidal basin :—

	Spec. 4			5		6		7		8		9		10	
IV.	1+1	1+1	1+1	1	1	1	1	1+1	1	1+1	1+1	1+2	1+1	1+3	
III.	1+4	1+2	1+?	1+4	1+?	1+?	1+1+?	1+4	1+2+?	1+1	1+4	1+3+2	1+3+?	1+4	
II.	2+3	5+1	5+2	1+2	5	2+5	6	5+6	4+1	5	6	6	6	5+2	
I.	The forceps show no definite variations, but apparent shape varies with degree of separation.														

Number 9 is about half the diameter of the others, which are of approximately the full size. 10 is a little larger than 9.

In specimen 4 I found the following formula before dissection of the plates :—1-1:1-1:4-4. After dissection it was clearly 1+1-1+1:1+4-1+2:2+3-5+1 as entered on table above.

In specimens 1.5.6.7.8.10, maxilla III, while retaining its usual size and shape, is without all or most of its smaller teeth. The character of its material, the sharpness of the remaining fang (and denticles in 6 & 8 & 10) and the rounded appearance of the toothless edge indicate that they were probably never developed in these individuals.

The proportions of the feet have already been alluded to. There are no setæ projecting from the dimples which represent them in the first 6 to 20 segments, all apparently having been broken off short. The feet of the middle region are short and truncated distally, with short and thick posterior lip of seta-sac, while those of the posterior region are conspicuously long and often, but not always, crowded together through the shortness of the segments in this region. The finger-like lobes they carry are conspicuous (see text-fig. 75-77). The dorsal tubercle (text-fig. 76) is retractile and often not to be made out, and its fine setæ are often confused with muscle-fibres.

The setæ fall into five groups:—

1. Long capillaries. These, when not broken away, project well beyond the seta-sac lip, as shown in text-figs. 75-77. They are slender, slightly bent, and but little broadened and end in an extremely delicate flexible thread. There are no teeth or distinct wings or other markings, but a few are brown in colour with a granular surface.
2. Short capillaries, of extreme delicacy, projecting only so far that their ends lie among the shafts of the long capillaries. Whether these are really a distinct form, or, as Fauvel suggests, are newly made and partially extruded long capillaries I am not able to determine.
3. Aciculæ. These are light-coloured like the capillaries and, as shown in the figures, form a close bundle of five or six setæ distinguishable from the shafts of the capillaries through their lying at a different angle. Some of these are simply and rather bluntly pointed, others drawn out to a fine point, and in others again these are bent, as shown *in situ* in text-fig. 76.
4. Fine hair-like aciculæ of the dorsal tubercle.
5. Acicular setæ, one to each foot ventrally. These are characterised by being swollen and brown coloured distally. Many have a peculiar transparent cap distally, with an appearance of being hollowed out beneath it, but this cannot be made out in all, even in adjacent feet. Two forms of this seta, from the 110th and 112th feet, are shown in text-fig. 78.

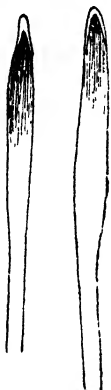
The anus is slightly dorsal, being at the end of a small tubercle which breaks through the last minute segments. In some specimens there appears to be a large anal funnel, but this, on examination, turns out to be a series of young regenerating segments.

There are no appendages. One specimen seemed to have about ten tubercles round the aperture, but comparison with other specimens showed that these were merely fortuitous wrinkles.

This species is possibly identical with Grube's *Arabella planiceps* from the Philippines, which is of similar size, has the

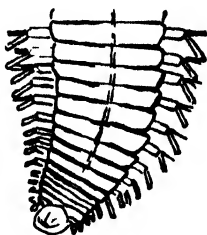
same semicircular prostomium, inconspicuous anterior feet, and long flexible ends to the setæ of the posterior part of the body. The setæ of the anterior part are, however, described and figured by Grube as bent and broadly bordered; such have not been found in these specimens, and the conspicuously long feet and

Text-figure 78.



*D. major*.—Two forms of acicular setæ from neighbourhood of 110th foot.  $\times 70$ .

Text-figure 79.



Posterior end showing long feet and anal funnel.  $\times 10$ .

long top of the seta-sac, which are so constant in *D. major*, are not noted in *A. planiceps*. Grube's description is much too brief for certain identification in any case, and his figures do not inspire confidence. The jaws are not figured at all.

#### *DRILONEREIS LOGANI*\*, sp. n.

The non-existence anteriorly and minute size of the feet posteriorly are striking.

Body extremely long and slender, even for this genus. A specimen 0.75 mm. in width would, if complete, probably attain to 1000 segments and a length of 25 cm.

Segments short anteriorly, length equal to or double the breadth posteriorly.

Prostomium a pointed triangle, flat, with groove in mid-dorsal and ventral lines. Former extends on to peristomium, which is hardly distinguishable from prostomium dorsally.

Pincers of jaws *denticulated at tips*, bases with three long teeth.

Setæ generally absent. When found straight and simple in

\* After my friend J. Gordon Logan, Esq., to whose help I owe, among other finds, the long series of *D. major* and the interesting variety of *Arabella novecrinita*.

anterior feet, of very characteristic form in posterior. Strong acicular setæ in anterior feet.

The following specimens were collected :—

2 fragmentary, from Suakin Harbour.

1 head and 56 segments from Wasin, Kenya Colony, 10 fathoms.

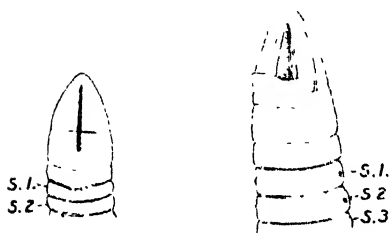
The sizes are :—Suakin Harbour, 0·75 and 0·4 mm. wide. Wasin about 0·3 mm. The former is 13 cm. long with 412 segments, the second 9 cm. with 227 segments.

The largest is more than four times the bulk of the smallest, and as the latter was collected separately and at a distance from the others, we may be assured that the peculiarities of the jaw apparatus and feet are not accidental but real specific characters.

As several fragments are preserved equal in length to those

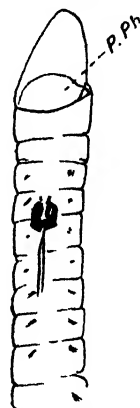
Text-figure 80 a.

Text-figure 80.



*D. logani*.—Dorsal and ventral views of specimen no. 1, from Suakin.

S<sub>1</sub>, S<sub>2</sub>, S<sub>3</sub>. First three setigerous segments, × 14 and × 18 respectively.



The minute Kenya Colony specimen seen as a transparency. P.Ph., the partly protruding pharynx. × 25

bearing heads and perfectly uniform, showing no approach to a tail, we may conclude that a complete specimen (if one could ever be collected) might attain to 800 to 1000 segments and a length of 25 cm. or more.

The body is narrower in front, widens gradually to about the 15th segment but rapidly from this point to the 22nd, where it reaches its maximum, which soon, however, falls to the general breadth. These widths are for the two larger specimens :—

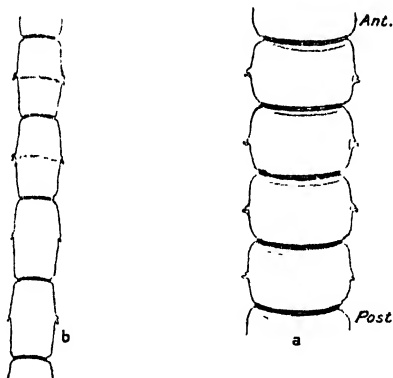
At peristomium .....	0·6 mm. and 0·4 mm.
15th segment .....	0·75 mm
Maximum .....	1·0 mm. and 0·5 mm.
General thereafter .....	0·75 mm and 0·4 mm.

Where elongated segments occur the breadth is reduced by about a tenth.

As shown in text-figs. 80 and 80 *a* the anterior segments are comparatively short but they soon become much longer, as long as they are broad, and in the hind-body they occasionally elongate to double this length, and some are bi-annular. Examples are shown in text-figs. 81 *a* & *b* which also show the maximum development of the feet, which for the first 15 segments do not show even the little papilla of the seta-sac lip.

The prostomium is of the same shape and structure in all three specimens. Its shape and relations to the peristomium are given by text-figs. 80 & 80 *a*. Pro- and peristomia are practically continuous on the dorsal side, faintly distinguishable by the very slight brownish tinge and iridescence of the skin, of the peristomium. The edge of this skin is found when favourably lighted.

Text-figure 81.



*D. logani*.

*a*. Segments about 270th in specimen 1.

*b*. " " 140-180 in specimen 2.

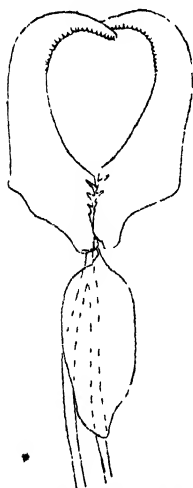
Both show maximum development of the feet. Both  $\times 18$ .

The appearance as seen by ordinary examination is given by the sketch in text-fig. 80. The dorsal and ventral grooves are conspicuous. In side view the prostomium is seen to be flat and about half the depth of the peristomium in thickness, as is usual in this genus. In certain lights it appears to be deeply hollowed underneath, but more careful examination shows that it is flat with only a central hollow. In specimen 2 this is a mere line. The border of the peristomium is straight. In this specimen the anterior third of the first ring is marked off by a vague line, S. 1. 2. 3. marking the first three setigerous segments in the figure. Above the anterior border of the peristomium is seen a small portion of the eversible pharynx.

There are no appendages or other sense organs.

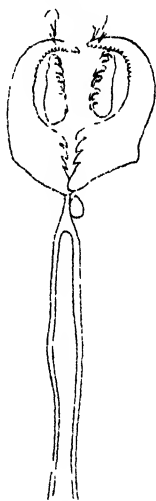
The jaws of the small East African specimen are shown in text-figs. 80 *a* & 83. They are black and brittle, and in the largest Red Sea specimen were found broken on opening the worm. This breakage showed clearly (1) the denticulations of the *points* of the pincers, a feature not seen in any other species; (2) the shape of the main toothed plate, with its long anterior teeth in a plane vertical to that of the plate, so making a two-pronged fork (an arrangement frequently seen), but in neither of the Red Sea specimens can I make out teeth on the anterior plates. In that from Wasin they are found to be two pairs of simple prongs. The articulation of the bases of the pincers is as in the Wasin specimen but more developed. Text-fig. 82 shows this structure as found in

Text-figure 82.



Pincers and supports.  
Suakin specimen no. 2.  $\times 200$ .

Text-figure 83.



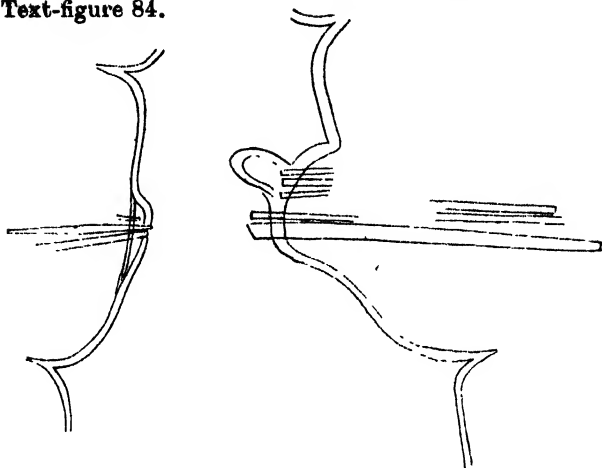
The complete apparatus in the Kenya  
Colony specimen.  $\times 200$ .

the Red Sea specimens. Ventrally the two pincers have a massive and asymmetrical articulation, to which the shield-shaped third support is joined by a slender thread. The junction of the long supports is shown by dotted lines, the articulation of the plates being dorsally much narrower and simpler. The denticulation of the ends of the pincers is visible in this specimen, mounted in the body, but details are drawn from the other specimen in which they were removed. The round accessory support is here shield-shaped, larger in proportion, but of the same type.

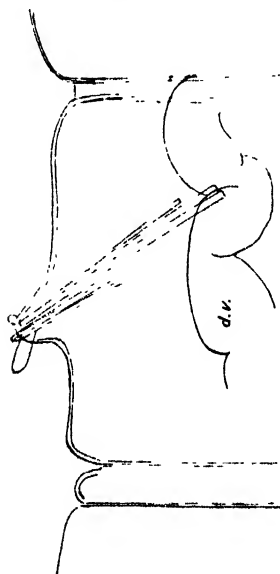
The development of the feet is illustrated by text-figs. 80, 81, and 84-86, and has been referred to above. In all figures they are represented as seen from above. It is to be noted that text-fig. 86 showing the maximum development of the feet,

Text-figure 85.

Text-figure 84.



Text-figure 86.

*D. logani.*

Feet 7, 20, and 225 seen in optical section.

Scales:  $\times 200$ ,  $\times 300$ , and  $\times 150$ .

emphasised slightly by pressure on the coverslip, is of half the scale of the others. In it, *d.v.* marks the dorsal blood-vessel which lies in coils, showing that even these segments, as long as broad, are contracted.

Unbroken setæ are extremely rare; even the points of the aciculæ and acicular setæ are worn down level with the thick and tough epidermis. The three figures from specimen 2 of the Red Sea show the short swollen acicular setæ of anterior feet, much larger, but less conspicuously swollen in the 20th segment (text-fig. 85). In segment 225 (text-fig. 86) this and the aciculæ are not distinguishable, being more slender and conspicuously long inside the body, almost meeting these from the other side under the dorsal vessel.

Text-figure 87.



The only two unbroken capillaries found, and point of acicular seta.

Foot 400.  $\times 300$ .

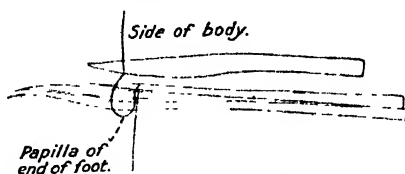
Examination of hundreds of segments reveals only an occasional acicular seta or a slender hair-like capillary, but two complete and well projected capillaries were seen and found, under a high power, to be of a striking shape. Their disproportionately long, slender tips apparently are the hairs more frequently seen, the blades below them being usually below the surface of the skin (text-fig. 87).

For anterior setæ I can only show those of the Wasin specimen. Here again, setæ, except the relatively enormous aciculæ, are almost always missing, but two were discovered, of a very simple type, in the 45th foot (text-fig. 88). It is unfortunate that only 56 segments of this specimen were obtained; one would like to have seen more of the strikingly formed capillaries of the hind body.



Judging by the relative sizes of acicular and capillary setæ and the almost entire absence of the latter through wear, it seems likely that they are vestigial structures of little or no importance to the animal.

Text-figure 88.



*D. logani*.—Setæ of 45th segment of the minute Kenya Colony specimen showing the enormous acicular seta, one complete acicula and base of second, and two of the three capillaries.  $\times 300$ .

### The Genus ARABELLA.

Only twelve species have been recognisably described, of which two, *A. (Aracoda) obscura* Willey from Ceylon, and *A. iricolor*, of the Atlantic and English Channel, are confined to the Old World, and one, *A. (Aracoda) multidentata*, is common to the Atlantic, Pacific, and Indian Oceans, having been discovered by Ehlers in Florida, and later recorded by Augener from S.W. Australia and Amboina. These collections now add an Indian Ocean species with varieties in the Red Sea and Cape Verde Islands.

The objection made above to the creation by Chamberlin of a new genus *Cenothrix* received emphasis a few days later from my finding the guarded acicular setæ upon which Chamberlin lays such stress, in the species of *Arabella* hereafter described from Professor Gardiner's Maldivan and my own collections from the Red Sea and Cape Verde Islands. This species resembles Chamberlin's very closely but, except in one variety, has the hooked posterior plates of the upper jaw characteristic of the genus.

Though there is no question of the reality of the hooded acicular setæ described by Chamberlin, and found in all these specimens, a broken or distorted capillary may somewhat closely resemble them. Such a case is figured on page 79, and in any case their derivation from the winged capillaries is obvious. It is possible, therefore, that less perfectly developed forms of the same structure have been overlooked in other species.

As collections rarely contain more than one specimen of any species of this interesting genus, little has hitherto been possible towards working out variation of species, of which this series shows extraordinary examples.

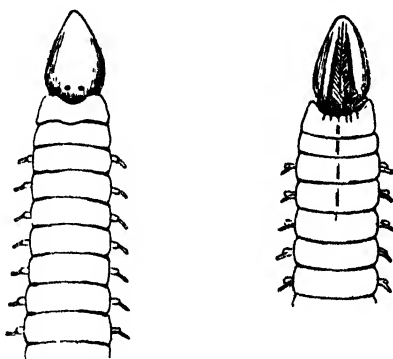
It is notable that these collections do not contain the Atlantic form *A. iricolor*, which Fauvel records from the Red Sea and Indian Ocean. The absence of the Mediterranean and Atlantic *Drilonereis filum*, which Fauvel also records, is noted above.

*ARABELLA NOVECRINITA*, sp. n.

The species is like, and probably identical with, *A. (Cenothrix) mutans* Chamberlin, a single specimen of which was brought from the shore of Easter Island \*, in spite of the fact that all my sixteen specimens but three differ markedly in the jaw apparatus. In *A. mutans* the proximal pair of plates is asymmetrical, only one (the right) being formed into a hook anteriorly, and this appears to be ill-formed, while the left plate is toothed throughout its length. In *A. novecrinita* the jaws are almost perfectly symmetrical, in var. *logani* the first pair is nearly so, the second asymmetrical; in var. *asymmetrica*, while one of the first pair ends in a long slender hook as usual, the other is toothed through nearly its whole length, thus approaching the condition of Chamberlin's specimen and also the genus *Notocirrus*.

The prostomium is a pointed cone with the usual four eyes at

Text-figure 89.

*Arabella novecrinita*, sp. n.

Dorsal and ventral views of the forepart.  $\times 10$ .

its base (text-fig. 89). Peristomium in two clear rings, sometimes indistinctly separated dorsally, anterior border slightly recessed in mid-dorsal line, wrinkled ventrally. Feet all prominent, though small. Dorsal cirræ rudimentary. All have a large finger-shaped lobe ventral to the seta-sac projecting postero-laterally, sometimes upwards. Setæ include (1) capillaries with narrow plain borders, (2) with broad borders bearing denticles proximally, (3) acicular setæ with peculiar asymmetrical hoods.

Of the typical form the collections contain

Two specimens from Minikoi (Stn. 1), Maldive Is.

One specimen from Chuaka Bay, Zanzibar.

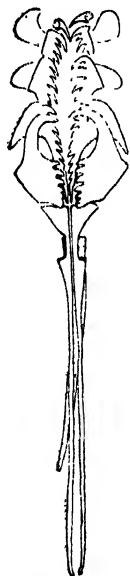
The former, though perfectly preserved, lack nearly all their

\* Chamberlin, Mem. Mus. Comp. Zool. Harvard College, xlviii. 1919, p. 329.

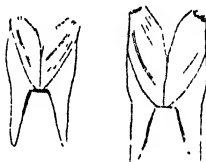
setæ, though such as remain agree exactly with those of the Chuaka specimen, and, as other characters are the same, there is no doubt of their being one and the same species and variety. The body is peculiarly round, with long segments and widely separated feet throughout its length. It tapers gradually towards the head, but more rapidly at the tail end.

The two complete specimens measure 19 cm. and 11 cm. in length, with a maximum breadth of about 1 mm., with 317 and 280 segments respectively. The first ten segments are three times as broad as long, but in the middle region (and most of the body) about twice as broad as long.

Text-figure 90.



Text-figure 91.



Lower (mandibles), from Zanzibar and Minikoi.  $\times 30$ .

*A. novecrinita*.—Jaws, symmetrical type.  $\times 40$ .

The feet (text-figs. 89 and 92–93) are all small but quite distinct, measuring about one-fifth the breadth of a segment when the seta-sac lobe is included. This projects from below the setæ as a finger-like process, generally pointing rather backwards and upwards, and is rather longer than the foot itself. It is best shown in the figures of the anterior end of the worm, as in those of the feet and setæ it is compressed.

The prostomium, as usual in this genus, is an elongated cone, round in section, but for a narrow flattened area (in one specimen a narrow groove) ventrally. It bears the usual two pairs of eyes

at its base, all of the same size, but the median pair, being nearer the surface, is the more conspicuous in the Minikoi specimens; but in the Zanzibar specimen, which is more transparent, they are all alike. (This may explain the variation found by Treadwell in the relative conspicuousness of inner and outer pairs of eyes.)

The peristomium consists of two unbroken rings, of which the first is rather the longer. It is notched just behind the eyes, but nuchal-pits are not visible. Ventrally it is slightly wrinkled behind the mouth, but in one specimen these wrinkles are inconspicuous.

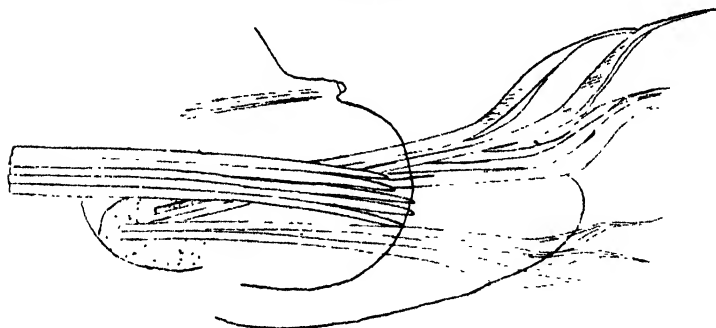
The jaws are symmetrical in all three specimens, the formulæ of two\* being

4—1.	1—1.
4—4 ? 5.	5—4.
4—4.	5—5.
2+9—2+9.	?—1+9.
1+5—1+6.	1+6+1—1+6+1.

For the shapes and relations of the plates see text-fig. 90, which shows that they are much more of the form normal in the genus than are the plates in *A. mutans*, which, from Chamberlin's sketch, seem to be degenerate. The supports are as usual, but the broad articulations to the pincers and slightness of the angle, where in *A. iricolor* is an upturned spur, should be noted.

The lower jaws are best described by text-fig. 91.

Text-figure 92.



*A. novocrita*. Suez specimen.—20th foot, smooth bordered capillaries only.

× 75.

The feet are nearly the same throughout the body, they and their finger-shaped ventral lobe being conspicuous from the first. The dorsal tubercle is visible under the microscope (text-fig. 92), but is never conspicuous as in *A. iricolor*.

\* The jaws of one specimen have been lost in the interval since 1904, but their symmetry was noted in that year.

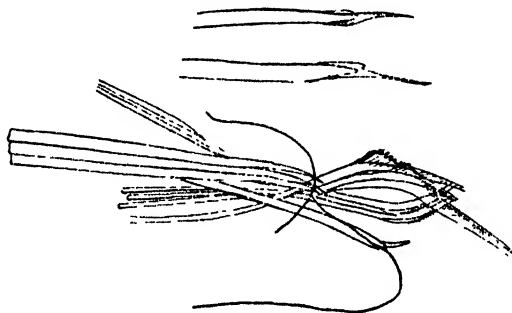
The setæ comprise:—

- (1) A bundle of fine aciculæ in the dorsal tubercle.
- (2) Large aciculæ sometimes with fine points.
- (3) Acicular setæ with asymmetrical and rudimentary "hoods."
- (4) Capillaries, slightly bent, narrowly bordered, the borders plain or finely denticulated.
- (5) Capillaries distinctly bent and broadly bordered at the bend, where the border bears about four teeth.

All are slightly yellowish in colour, including the aciculæ and acicular setæ.

Numbers 3 and 5 are absent from anterior feet (e.g., text-fig. 92), but all are present as early as the thirtieth segment (text-fig. 93). The aciculæ number three in each foot anteriorly, two posteriorly. The capillary setæ five to seven anteriorly (generally only five), three (sometimes four) in the posterior feet.

Text-figure 93.



*A. novecrinita*. Zanzibar specimen.—30th foot, all the kinds of setæ present.

× 80.

Above: Two of the hooded acicular setæ from region of the 250th foot. × 220.

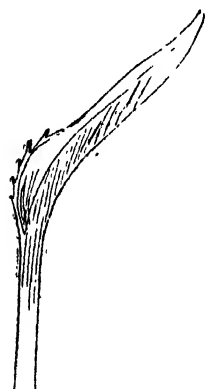
The denticulated form (text-fig. 94) never exceeds two, and there is only one hooded acicular seta in any foot, though two are seen occasionally. All these bordered setæ are striated obliquely, and in many cases the setæ break along the striæ. The denticulation of the edge and the breadth of the border vary. In some the border is hardly visible and the edge of the seta smooth, in others broad with coarse denticulation. There are thus at least three kinds of capillary in each foot. The larger denticulations are distinct, and definite in number, five, sometimes four, per seta; but there is a variety (shown in text-fig. 95) with smaller and more numerous denticles continued distally by minute and indistinct denticulation. This kind of seta is exceptional in the type, but is the rule in var. *logani*. One of the plain bordered setæ of the dorsal bundle is distinctly larger and longer in the bordered portion than in the rest, and in the anterior feet, where all the setæ are plain bordered, this special

form is still distinctly recognisable. The hooded acicular setæ (text-fig. 93) occur singly and ventral to the others; in the posterior feet they sometimes project a long way and are especially distinct, but they are always easily found. They correspond exactly with Chamberlin's drawings, as do the other setæ save for the greater breadth of the borders in these specimens.

The denticles on the bordered setæ are so slender and lie at such a small angle with the border, and furthermore are duplicated by the other wing, that they are difficult to make out in detail. Those shown *en face* in figure 98 were the most easily made out.

The tips are almost invariably damaged, as shown in the

Text-figure 94.



Text-figure 95.



*A. novecrinita*.—Denticulated capillaries. To left: The form usual in the species (from foot 100, Zanzibar specimen). To right: An exceptional variety, from 30th foot.  $\times 300$ .

figures. Only after careful searching were two younger setæ discovered provided with the slender tips shown in the figures of var. *logani*.

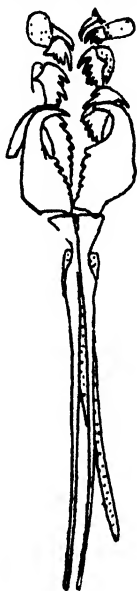
The anus is provided with four short cirri in the Zanzibar specimen, but they are absent in the complete specimen from Minikoi. One pair arises from swollen bases as in *A. iricolor*.

#### *ARABELLA NOVECRINITA*, var. *LOGANI*.

A single specimen of good size was collected for me by J. Gordon Logan, Esq., at Suez in 1905, and differs sufficiently from the preceding to warrant separate notice as a named variety.

(1) The body-form is more contracted, i. e., more like that of other worms, than in the Indian Ocean specimens (including Chamberlin's species from Easter Island)\*. The pro- and peristomia remain the same, though the dorsal recess on the anterior border of the peristomium is scarcely visible, but after that the body rapidly broadens out to a maximum of 2 mm., and is somewhat flattened ventrally for the first half of its length and on both sides in the tail region. The taper to the tail is gradual, suggesting regeneration, which would explain the fact that, in spite of its 2 mm. breadth and the larger size of its feet and setæ,

Text-figure 96.



*A. novecrinita* var. *logani*.—Asymmetrical maxillary apparatus (from a Cape Verde specimen).

its total length is only 9 cm. and number of segments only 196. There is no other evidence of regeneration, however. There is an anal tubercle but no cirri, as in the Minikoi specimen.

(2) The segments are short, being four and five times as broad as long.

(3) The jaw apparatus differs markedly in that the second maxillary plates are asymmetrical, as shown in text-fig. 96 and others.

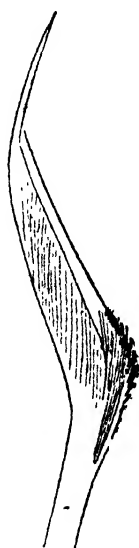
\* This difference may to some extent be due to the slow death of the worms collected in the Tropics due to overheating of the water during their conveyance to the laboratory ashore.

The teeth number

1—1.  
 1+3—1+3.  
 1+3—1+5.  
 1 (double)+12—8. Asymmetry.  
 1+7—1+7. Partial symmetry.

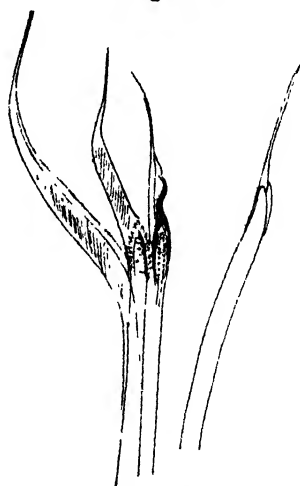
It is to be noted that this asymmetry is not merely the loss of the long and narrow descending part of plate II, as the teeth differ distinctly in the shape of their upper ends, the short plate on the right side being curved over the end of the forceps to a much greater extent than is the head of the large plate on the left.

Text-figure 97.



Var. *logani*.—Denticulated seta from 100th foot.  $\times 300$ .

Text-figure 98.



Group of setae from 180th foot: Two denticulated setae seen *en face*.

The lowest plates both end in large hooks, but are not quite so symmetrical as in the Minikoi and Zanzibar specimens.

Exactly the same asymmetry of maxillæ II is figured by Ehlers for his *A. quadristriata* in 'Die Borstenwürmer,' and by De St. Joseph under the name *Maclovio gigantea*. As these names are synonymous with *A. iricolor*\* we have precedents for placing this specimen in one species with the type, which I confess I am glad to have in view of the even more difficult case which follows.

\* McIntosh in 'British Annelids,' and other authorities.



The setæ differ in that:—

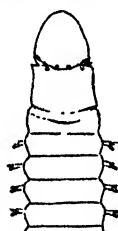
- (1) The aciculæ are more numerous, five instead of three in anterior feet, three instead of two in posterior. They do not always carry the fine points usual in this species.
- (2) Capillaries usually eight in anterior feet, instead of five, four or five in posterior instead of three (or four). Two per foot are denticulated as usual.
- (3) Of the two types of denticulated setæ noted in the Zanzibar specimen the second (compare text-fig. 95 with text-fig. 97) is here typical.

These variations are figured. Text-fig. 98 includes (1) the larger plain (or *finely* denticulated) bordered setæ; (2) the two coarsely denticulated setæ seen from in front with the two wings or borders opened out in one case, closed in the other; (3) the hooded acicular. Text-fig. 97 shows the usual side view of a denticulated seta, while text-fig. 92 of an anterior foot shows plain bordered setæ and aciculæ only—in this case the aciculæ do not carry the long points usually present and shown in text-fig. 93. Except for the number of setæ present, this figure will serve for either type or variety.

#### ARABELLA NOVECRINITA, var. ATLANTICA.

Of the eleven specimens collected in the Cape Verde Islands only two were seen alive, the remainder being collected from the masses of worms and crustacea obtained by washing out dredged

Text-figure 99.



*A. novecrinita* var. *atlantica*.—Anterior end of a specimen in which

- (1) Peristomium forms a collar round base of prostomium, through which lateral eyes are seen.
- (2) Dividing line between first and second rings of peristomium, though clear ventrally, is broken and doubled and indistinct on dorsal side.

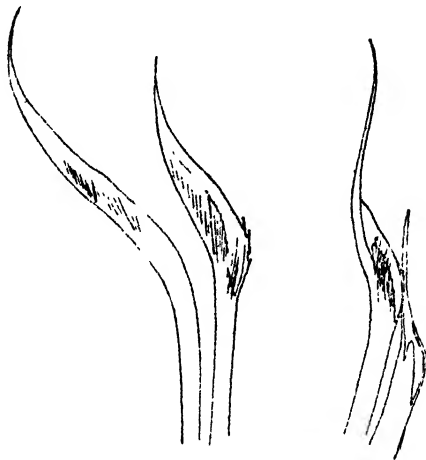
material and the incrustation of *Vermetus* and *Lithothamnium* which coats all rocks at low tide\*.

The colour in life is the usual flesh-colour of the Lumbri-conereidæ, but lighter and yellowish. The second specimen is

\* See "Ecology and Deposits of the Cape Verde Marine Fauna," by the author, P. Z. S. 1906, vol. i.

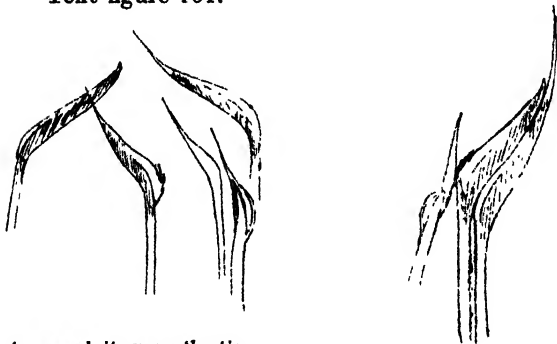
noted as "pearly." The fore-part is very extensile, and when extended decidedly narrower than the hind part, and so trans-

Text-figure 100.

*A. novocrinita* var. *atlantica*.

Text-figure 102.

Text-figure 101.

*A. novocrinita* var. *atlantica*.*A. novocrinita* var. *asymmetrica*.

Setæ. Scale, all  $\times 300$ , from which relative sizes of the specimens may be seen. In figs. 100 and 102 setæ are in positions occupied in the feet. Feet are 100th, 95th, and 70th respectively. In fig. 100 second seta from the right is a deformed capillary which strongly resembles the acicular seta next to it.

parent that the delicate long supports of the jaws are visible under a lens. This great contractility is evidently the cause of

the marked variation in the proportions of the body found in the preserved specimens. In none is the forepart so markedly narrower than the rest as it was in life. Of the four eyes the outer are, in life, the larger. The shape of the prostomium appears to have been the same as in the preserved specimens.

This specimen, in its proportions, is intermediate between the type and var. *logani*; others are much more contracted, so that the prostomium is withdrawn into a collar formed by the peristomium. On pulling this back the prostomium and eyes are found to be of the normal form, though in some the anterior end is broader (see text-fig. 99).

In some specimens the fore-body shows a telescoping of the segments into each other, but behind they remain long and the feet well separated. In one all remain long. The characteristic V-shaped mark on the ventral surface of the prostomium is present, and the peristomial dorsal recess is generally to be made out. The jaws are asymmetrical exactly as in var. *logani*, and the numbers of teeth approximately the same, *e. g.* :—

$$\begin{array}{r} 1-1. \\ 1+?3-1+4. \\ 1+5-1+4. \\ 10 \text{ to } 12-6. \\ 6-6. \end{array}$$

Indeed the only difference from var. *logani* is in the setæ, where, in all the Cape Verde specimens alike, including var. *asymmetrica* below, the denticulated setæ are shorter in the head or bordered portion. There is only one to a foot, with three or four denticulations. The series figured (text-figs. 100-102) shows their close resemblance in specimens of different sizes and in var. *asymmetrica*. The figures show the resemblance between the other setæ and those of the type and var. *logani*, and also that the hooded aciculars are of uniform pattern right through.

#### A. NOVECRINITA, var. ASYMMETRICA.

The smaller specimens from 0.25 mm. to 0.6 mm. in breadth were specially examined. Three were found to have a third type of jaw apparatus, while agreeing with var. *atlantica* in other respects. Two of the specimens were found with the nine of *atlantica* in W. 9 and one alone in W. 13.

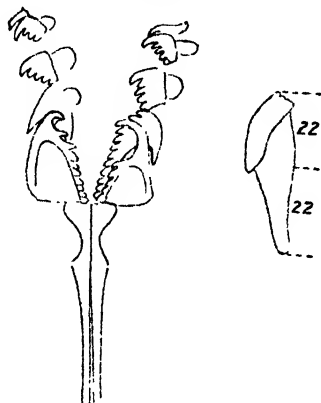
This peculiarity of the jaw apparatus would be sufficient grounds for the creation of a new species (or genus even), but I have been unable to correlate it with a single constant difference to the other varieties.

The upper jaws are sufficiently described by text-figures 103 and 104, from which it is seen that the right plate is toothed almost through its whole length. There is, however, always a diastema below the anterior hook. (This variation is parallel to that found in the small asymmetrical posterior plate in

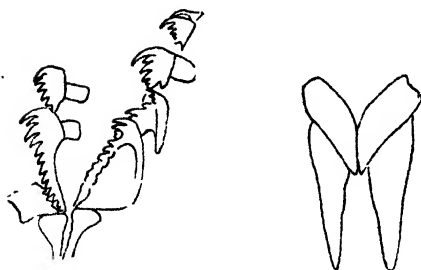
*Enone fulgida*, which may be evenly toothed throughout or end in a small but distinct hook\*.)

The second pair is also asymmetrical exactly as in vars. *logani* and *atlantica*. Allowing for differences due to the different angles at which the plates are seen under the microscope, the upper series are found by careful focussing to be alike in all specimens in any variety.

Text-figure 103.



Text-figure 104.



*A. novecrinita* var. *asymmetrica*.

Jaws of two specimens. Figures at sides of mandibular plates indicate proportions of lengths of upper plates to roots.

In fig. 103 (maxillæ) the square ends of the teeth are apparent only, and due to point of view.  $\times 95$  and  $\times 190$ .

The lower jaws differ markedly from those in the other varieties in the length of their posterior projections, which are sometimes longer than the anterior plates.

Had we but one or two specimens of each variety the difference

\* Compare also *Onuphis brittanica* McInt. Brit. Annelids, pl. lxx. fig. 13.

in the jaws would make this a new species, but on examining a series we find that this distinctive difference of the lower jaws is shared by specimens which have the typical *atlantica-logani* upper plates, and in fact we have a continuous series between the extremes. Compare the following of the smallest specimens\* :—

A. var. *asymmetrica*, specimen W. 10, 0.36 mm. wide.

Prostomium blunt at end but with the usual V-shaped mark below. Peristomium also normal. Body round and segments long.

Jaws, upper, fully asymmetrical; lower, with supports as long as the anterior plates.

Specimen W. 9. 1. Pro- and peristomia as usual, but anterior segments of body short, posterior long.

Upper jaws exactly as in the preceding. Lower with long supports, but still *shorter than the end plates*.

Specimen W. 9. 2. 0.25 mm. wide. Prostomium blunt-ended and when mounted in glycerine only two eyes can be made out, which are large and light brown in colour, an effect possibly due to long preservation. Segments short throughout the body.

Upper jaws completely asymmetrical, the plate with the short upper hook has this doubled.

Lower jaws with long supports *equal* in length to the narrow upper plates (text-fig. 104).

This being the smallest specimen of all the setæ are completely figured, but no definite difference to the others, or of var. *atlantica*, is to be seen.

B. var. *atlantica*. W. 9. 3. 0.5 mm. broad.

Body contracted. Upper jaws with a long diastema, as in text-fig. 105, which is from specimen W. 9. 5. Specimen 4 is the same, and all are in fact as in vars. *atlantica* and *logani*, but the lower jaws are of the type found in var. *asymmetrica*. In No. 3 the supports are  $\frac{1}{6}$  longer than the upper plates (measured vertically); in No. 5 they are  $\frac{1}{5}$  longer. In No. 4, however, the relation is reversed, being as 7 is to 5, thus leading to the relations found in adults of all varieties. Variation in the breadth of the anterior plates is also shown in the figures.

The succeeding four specimens from the W. 9 series show no variation from the type in either upper or lower jaws.

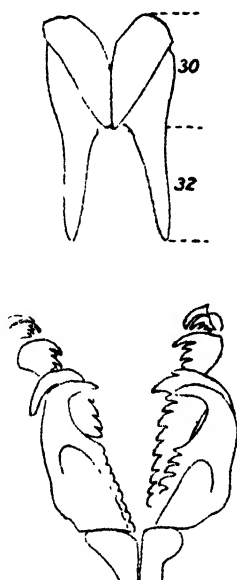
It seems clear that these varieties of lower jaw are merely juvenile characters, and it is tempting to regard the toothing of the whole plate in var. *asymmetrica* as an ontological repetition of the evolution of pincers from a uniformly toothed plate. It is

\* In the smallest specimens examined details were clearly and easily made out, as the plates were dark brown in colour and somewhat translucent. In rather larger specimens they were as usual jet-black and quite opaque, and the difficulty of separating and arranging the plates when the whole apparatus is hardly visible to the naked eye is considerable. It may be overcome by bleaching for some hours in a mixture of  $H_2O_2$  and  $NaOH$ , by which brown plates are obtained instead of black, and at the same time of less rigidity, so that they lie flat on the slide instead of with the toothed edges of the wedge-shaped plates directed upwards and consequently invisible.

probably reversionary, but is not a normal development since (1) we find no intermediates between the var. and type as we do in the case of the lower jaws; (2) Chamberlin's specimen, possibly the same species, was quite large, 1.6 mm. in diameter without the feet.

These variations of the jaw apparatus within a single species are almost as remarkable as those described for *Ænone fulgida*. I need hardly say that I have been driven reluctantly by the facts to include all in one species, after consideration of the opinion of Professor Treadwell, who, by confining himself to this one group, has had a greater experience of it than any other

Text-figure 105.

Jaws of a specimen of var. *atlantica*.

Upper jaws normal, lower long-rooted.  $\times 95$ .

worker. After his large and important work on the West Indian Leodicidæ, he states: "I have found that while such details as the number of teeth in a plate may vary, the general appearance and the arrangement of the parts of these structures are decidedly characteristic in any species." In the following year, after examining the large collection he made in Fiji and Samoa, he adds: "Later study has led to no conclusions different from those there stated, unless it is to further emphasise the importance of the jaw in classification. I found the general character of the jaw remarkably constant in any one species, especially in the form of the plates and their colour."



1868. Ehlers changes *Aglaura* to *Aglaurides*.

1878. Grube describes Savigny's species as *Aglaurides fulgida* from the Philippines.

Numerous other genera founded for the same two species.

1900. Gravier describes the Red Sea species under the name *A. erythræensis*, but is corrected by Fauvel in 1917.

March 1904. Specimens of "*Halla*" from Naples and the Cape examined by me and compared with Maldivan and East African examples. None but differences of specific rank exist.

A remarkable variation, by which the jaw-plates become symmetrical, discovered in one of the Maldivan specimens.

November 1904. Specimens examined alive at Suez with a view to determining maximum normal expansion of the nuchal organs.

The above results not published till present date.

1917. Fauvel discusses the whole synonymy and admits only one genus *Aglaurides* with three species. *Halla parthenopeia* not considered.

? 1922. Treadwell, adopting a suggestion as to rules of priority from Chamberlin, gives the name *Ænone* to the whole genus. Describes *Æ. diphyllidia* with special care.

1923. Author discovers another variation of the jaw-plates (in Zanzibar specimens) and divides the genus thus (provisionally as regards *Æ. diphyllidia*):—

#### Genus *ÆNONE*.

Tentacles long and always visible; nuchal organs small. *Ænone parthenopeia*.

Tentacles short, generally hidden ..... *Æ. fulgida*.

#### Species *Æ. FULGIDA*.

Jaw-plates symmetrical.

(1) by enlargement of the small asymmetrical plate . . . var. *diphyllidia*.

(2) by reduction of the opposite plate and the size of the asymmetrical . . . . . var. *malensis*.

Jaws asymmetrical as usual in the species, but in some anterior plates there are several long fangs . . . . . var. *arabelloides*.

Fischli's species, *Æ. pacifica* from Ternate, is so likely to be merely *Æ. fulgida* that I follow Augener in absorbing it into that species. The possession of two hooks on the second plate on the right upon which Fauvel lays stress is a not uncommon variation. Langerhans describes *Halla sulfurea* from Madeira (Zeitschr. f. wiss. Zool. xxxiii. 1880), which seems to differ from *parthenopeia* in having 6 eyes (one minute pair on the ventral side of the prostomium), shape of the lower jaw-plates, and the possession of *strongly* hooked setæ, with the usual capillaries. Until more material can be examined I regard the species as doubtful. Haswell's *Halla australis* has been shown to be *Ænone (Aglaurides) fulgida*.



**CENONE FULGIDA Sav.**

(Synonymy given under genus.)

With varieties:—*malensis*.*arabelloides*.

The following specimens were collected originally, others being added later from the coral reefs of the inlets of Dongonab Bay, Red Sea. The animal shows a liking for sponge habitats in comparatively stagnant water on reefs.

*East African collection.* 3 specimens, Wasin and Prison Island, Zanzibar.

*Maldives.* Hulule Male Atoll, 2 specimens.

*Red Sea: Suez Docks.* Among the lamellibranchs, etc. covering the dock walls. Under a crust of Polyzoa under a floating stage.

*Snakin Harbour.* Among coral and sponge.

*Dongonab Harbour.* Inner reefs, crevices of coral.

In the last-named habitat I found it quite common when employing labourers in obtaining coral for piers.

*Size.* Generally under a foot in length, but one specimen reached 480 mm. when alive. It is much shorter in spirit.

*Colour.* Orange above, bright yellow at sides and below. No markings. The colour darkens on exposure to air and in fresh water the worm secretes abundant mucus, which on addition of alcohol is stained violet by a second secretion. Alcohol dissolves out a quantity of this substance exactly as noted by Haswell for his *H. australis*, and for *O. parthenopeia* by Claparède.

Since my MS. was written in 1904, full accounts have been published, e. g., by Fauvel and Treadwell. The form and general coloration of the body are excellently given by the coloured plate of the living animal in Treadwell's "West Indian Leodicidæ." In life the prostomium also is exactly similar; it is only on examining the dental apparatus that Treadwell's species is seen to be distinct. It is remarkable that the species of this genus, *parthenopeia*, *diphyllidia* (= *symmetrica* Fauvel), and *fulgida*, should all be bright yellow or orange in colour when alive.

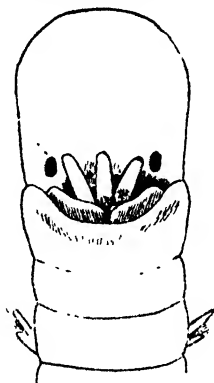
The prostomium, in spirit specimens, varies in shape as in text-fig. 107, in which the peristomium is cut away to show the tentacles and eyes.

The protrusion of the nuchal organs has not been observed since Savigny's time and does not appear to have been *figured* since, and my examination of numerous specimens alive and dead inclines me to believe that he figured an abnormality, if indeed the engraver did not add the organs acting upon verbal instructions. I give a figure (no. 106) of the head of a specimen which was quietly crawling in a basin. As I have frequently verified this drawing from other living specimens, I believe it represents the maximum *normal* protrusion of the organs.

The figure shows how greatly the prostomium differs from that of a spirit specimen, and the fact that all four eyes come to lie at nearly the same level when it is extended.

It is interesting to note that in a living but moribund specimen sketched at Suez, the prostomium and tentacles are retracted much as in spirit. The sketch is so like that on the right of text-fig. 107 that I do not copy it here, but the

Text-figure 106.



*Enone fulgida*. - Head of the living animal showing normal extension of tentacles and nuchal organs. (This specimen has a fifth eye.)  $\times$  about 9.

large eyes, contracted to a round shape, lay just outside the peristomial border, the smaller pair being visible through it. The tentacles were knob-like as in preserved specimens. Nothing could be more unlike the same parts in an active and undisturbed animal, or more likely to be made the type of an unnecessary species, or even genus.

Text-figure 107.



Head of two preserved specimens (from Kenya Colony and Zanzibar) to show variation in shape of the prostomia. Peristomia cut away as shown by dotted line to display eyes and tentacles.  $\times$  6.

To return to the normal extension of the parts. The peristomium is shown as lightly divided into two segments. If I had known that so much importance would later be attached to this point, I might have given it more attention, though, as it is admitted that traces of this division show in all specimens, insistence upon the question of its completeness or incompleteness seems a little pedantic.

The areas external to the large eyes are white, the rest of the prostomium being yellow.

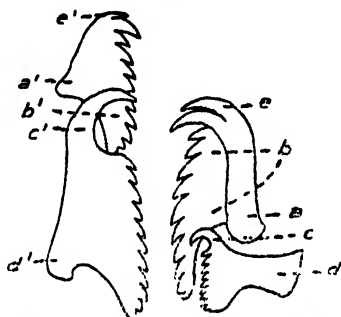
This specimen had a fifth eye as shown, but was otherwise quite normal.

Willey (Ceylon Pearl Fisheries, 1905) described a specimen in which there were two groups of three eye-spots each in place of the median pair of eyes.

Fauvel discusses the homologies of the small asymmetrical plate of the left-hand series. His figures, the most realistic ones published, give the usual arrangement, but I have been fortunate enough to find two rather abnormal specimens which definitely prove that each plate is homologous with its opposite in spite of the great differences in size.

In a specimen from Zanzibar which corresponds exactly with Savigny's account and especially with Ehlers' careful drawing from his '*Ænone diphyllidia*,' the arrangement of the last two

Text-figure 108.



Lower maxillary plates of a slightly abnormal specimen (from Zanzibar) illustrating the homologies of the pairs. Letters correspond on right and left sides.

pairs is slightly complex (see text-fig. 108). On the right is a long plate surmounted by two distinct long fangs, behind which, *without any interval*, are 10 smaller teeth. The strongest part of the plate is not at its posterior end as one would expect, but at the point marked (a) in text-fig. 108, which thickening continues into the two anterior fangs. The part b, bearing the smaller teeth, is much thinner and in an attempt to separate the various plates may break away along this line in one piece. The last plate of all bears 10\* very small teeth which are hard to make out, as they lie over the posterior part of the preceding and larger plate. The first is somewhat longer and more bent than the remainder, from which it is separated by a small gap.

On the left side these two plates are highly modified, the lower being so much enlarged that it appears rather to pair with the second of the right side, which it resembles in shape as well as in

\* The most posterior are very small indeed.

size, in not being drawn out so far in the transverse arm *d*. But its homology with the last plate on the opposite side is shown by the space between its first fang and the succeeding teeth. Also the plates *a* and *a'* show their correspondence by the presence of a second small anterior fang at *e'* as well as at *e*, and by its projecting at the inner posterior corner beyond the fang of the next posterior plate at *b* and *b'*.

One of the two specimens from Hulule in the Maldives differs from the above arrangement almost as much as if it were a distinct genus, the lower plates becoming almost completely symmetrical (text-fig. 109); though this makes a difference which is at first sight very striking the variation is a simple one when the above account of the homologies of the parts is understood. Further, in this specimen the two fangs of the right posterior plate, which are so characteristic of this genus and species, are here fused except at their tips, so that only one

Text-figure 109.

*Enone fulgida*.—Symmetrical jaws of the Maldivan specimen.

appears to be present until a careful examination is made. Both sides are alike in this respect also. Ehlers' figure of *Enone diphyllidia* shows only one anterior fang on the right posterior plate. Possibly two were really present (of which indeed there are indications in Ehlers' figure itself), but were confused as in the case above.

The jet-black colour and complete opacity of these small jaw-plates make their accurate examination somewhat difficult.

The following comparison of the numbers of the teeth is interesting:—

Abnormal specimen from Hulule.		Zanzibar specimen No. 1.		Ditto No. 2.		Grube's specimen. Philippines.	
1.	1.	1.	1.	1.	1.	1.	1.
5.	5.	6.	7.	4.	7.	5.	5.
8.	8.	5.	8.	7.	9*	6.	6.
10.	10 or 11.	8.	12.	9.	12†.	7.	7.
9 or 10.	10. v. small.	10.	9.	10.	8.	8.	11 or 12.

\* 2 of these very small.

† 5 of these very small.

The above table was made out in 1904. I have now examined the jaws of eight other specimens with the results given in the second table.

No other symmetrical specimen was found, but there is considerable variation not only in the numbers of the teeth but also :—

- (1) The prominence of the first hook-like teeth varies. In specimen nos. II and III the first teeth do not stand out beyond those succeeding them in the case of three plates on the left and all but the first on the right, where the first three teeth are of approximately equal length. This gives a very abnormal appearance to those plates, unlike that characteristic of the species, and recalling their arrangement in the genus *Arabella*.
- (2) The hook of the first plate on the left side (the small asymmetrical), which is given prominence in text-fig. 108 and in the text, is indistinct or absent—as in Fauvel's figure—in specimens I, III, V, VIII. It is not prominent in no. VI.
- (3) The doubling of the hook of plate II on the same side was not found in specimen I, and of course is disguised in II and III.
- (4) This feature on the right side was made out in specimen IV only.

*Table of variation of Jaw-plates.*

Locality.	Spec. no.	V.	IV.	III.	II.	I.
Zanzibar ..	1	1 1	1+4 1+5+1	1+5 1+7	1+6 1+8	1+7 8
"	2	1 1	1+3+1 3+1	4 2+2	4+1 or 2 12	?11 1+8
"	3	1 1	1+5 3+2	3+0 5	3+0 13	3+10 7
"	4	1 1	1+5+1 1+5	1+5 1+5	2+4+3 2+7	1+4+3 1+5+3
Dongonab Bay, Red Sea.	5	1 1	1+5+1 1+3+2	1+6 1+6+?3	1+6+2 2+8	1+6+2 7
"	6	1 1	1+3 1+4	1+4 1+5	1+7 2+8	1+6+2 7
Red Sea .....	7	1 1	1+4 1+4+1	1+4+1 1+5+1	1+5+2 2+10	1+8+3 1+5
"	8	1 1	1+4 1+5	1+5 1+6	1+5+4 2+7+4	1+5+1 8

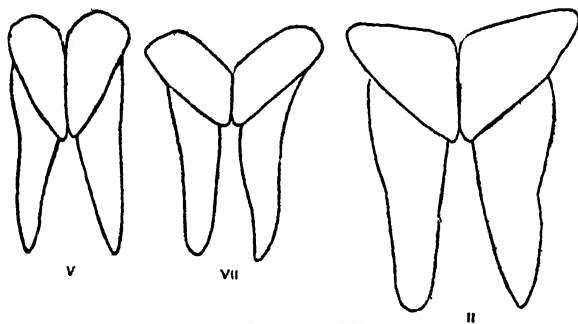
The first of each set of figures, which is normally 1, refers to the upper large hooks, the third to small teeth whether these occur anteriorly or posteriorly to those of more considerable development.

The lower jaws vary much in size and shape, as illustrated by the three sketches of text-fig. 110.

Of the eight specimens of the table, four have their mandibular plates more or less like the sketch to the left of text-fig. 110, three like the middle sketch, while the condition shown on the right was unique in specimen 11, in which it was noticed above that the upper plates were also peculiar. It should be noticed that the plates are not fused but merely hinged by ligaments, so that the divergence posteriorly of the same pair of plates is not constant.

As Fauvel shows, the parts of this upper jaw apparatus are not more or less flat plates as in e. g. *Ennece*, but are wedges

Text-figure 110.



(*Enone fulgida*.—Types of lower jaws (mandibles).  $\times 13$ .

The numbers are those of the specimens of the table.

bearing teeth along their ridges. The sides of the wedges are prolonged ventralwards for a considerable distance, these prolongations being readily distinguished from paragnaths, not only by their continuity with the "plates" but also by their jet-black colour. Paragnaths occur on the other—outer—side, and in this species are brown in colour. Gravier has confused these structures in his incomplete figure of the apparatus. I give a diagrammatic section of the jaw-sac, etc., drawn in 1904, in text-fig. 111.

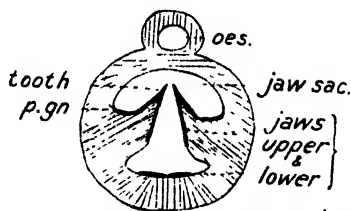
It is curious that the symmetry of the *Hulule* specimen is produced by the reduction in size of the right plate to that normal for the left, i. e. in exactly the reverse way to the symmetry of *Enone* (*Aglaurides*) *diphyllidia* as described by Treadwell and *A. symmetrica* (which is apparently synonymous with *diphyllidia*), in which symmetry is attained by the enlarge-

ment of the small plate. As Ehlers has described the normal form from Florida I am inclined to put all into one species, and make the variation of the lower jaw-plates a part of the specific description.

The variation of the mandibular plates shown in text-fig. 110 brings Treadwell's figure for *A. diphyllidia* within the limit of this species. There is always some strong white chitin at the angles, which is not, however, properly part of the jaw-plates and is not shown in my figures.

One of the specimens from Wasin, dredged from 10 fathoms, is only 1 mm. wide, and it is interesting to find so young an example exactly like the large ones except that the jaw-plates are dark brown, not black, and the dorsal cirri are small, smaller than the lip of the seta-sac. This is no doubt due to the easier access of the blood to oxygen in so small a body. The other characters were examined, but no difference from the adult form was detected.

Text-figure 111.



*Oenone fulgida*.—Diagrammatic section of the jaw-sac.

The species is thus recorded from the Philippines, tropical Australia, the Maldives, East Africa, Red Sea, San Thomé in the Gulf of Guinea, Florida and the West Indies, *i. e.* it is common to tropical seas, but is replaced by *O. parthenopeia* in the Mediterranean\*.

#### The Genus STAUROCEPHALUS (DORVILLEA).

Twenty species have been described clearly, and there is remarkably little synonymy. This is perhaps due to the small size and rarity of most species, *e. g.* those named by Grube in the "Annulata Oerstediana," and by Verrill fortunately remained untouched until rediscovered by Treadwell. To this number are now added two.

There are striking differences between species, but tabulation of these fails to indicate any natural grouping into subgenera. It may, however, be of assistance to future workers to note the following groups into which about half the species fall.

\* Langerhans describes *O. (Halla) sulfurea* from the Canaries which may be a young specimen of *O. parthenopeia*. I did not find an example of the genus in the Cape Verde Islands.

## I. Possessing a nuchal papilla.

*S. australiensis* McL.: see Treadwell, "Fiji and Samoa."*S. rubra* Grube: see Treadwell, "West Indian."*S. moniloceras* Moore, "Californian Annelids."*S. (Dorvillea) crassa* Chamberlin.*S. gardineri*, sp. n.

## II. Forked setæ present. Only one pair of eyes.

*S. kefersteini*. See McL., Brit. Ann.*S. pallidus*. " " "*S. ciliatus*. " " "

## III. Forked setæ present, but the usual four eyes.

*S. longicornis* Grube, "Ann. Semperiana."*S. polyodonta* Verrill: see Treadwell, *l. c.**S. incerta* Schm. (= *australis* Haswell).IV. Two species show features unique in the genus, viz. *S. rubrovittatus*, having extraordinarily overgrown brush or bristle-like teeth-plates in the outer rows, and *S. kefersteini*, having pulps of a length and slenderness not seen elsewhere.

The descriptions of the following species are practically useless: Grube's *S. filicornis* and *S. brevipinnis* in the "Ann. Semperiana," owing to omission of description of the jaws, *S. chajji* Clp. of the "Golfo de Naples," in which they are imperfectly described and indistinctly figured, and *S. rudolphii* Langerhans, from Madeira, in which the setæ are not figured.

The nearness to the ventral surface of the peculiar lower jaws is a curious feature. All here described, except *S. rubrovittatus* and the large *S. gardineri*, were picked out of "washings" consisting of hundreds of small worms principally Eunicidæ, Nereidæ, Syllidæ, and Phyllodocidæ, and in all cases these black forcep-shaped lower jaws were the first feature of the genus to be recognised.

These plates lie in the skin of the lower lip, their posterior processes lying a little deeper. They do not appear to be connected, or at most very lightly, with the large mass of muscle which carries the upper plates, and it is obvious that they cannot be protruded further than the position in which they are now found. The upper plates represent an early stage in the evolution of the Eunicid jaws, and it is interesting to find that in certain species, such as *S. similis*, described below, fusion has taken place between some of the plates at the proximal end of the row, resulting in a toothed plate like those of the Eunicidæ. This has gone further still in *S. polyodonta* Verrill, described by Treadwell, *loc. cit.*

## STAUROCEPHALUS (DORVILLEA) GARDINERI, sp. n.

The conspicuous features of this species, after its large size—it is gigantic for this genus—are the possession of a nuchal papilla and large transverse peristomial pits.



The possession of this nuchal papilla is shared by four other species, and the relationship of this one is best shown by tabulating the details which serve for specific discrimination, printing in italics those which *differ* from *S. gardineri*.

**A. Toothed maxillary plates in two rows on each side.**

I. *S. gardineri*, sp. n.

1. Tentacles jointed, same length as palps.
2. Maxillæ, inner row with long tooth on one side, outer row toothed both sides.
3. No terminal piece to dorsal cirrus.
4. Shafts of compound setæ not denticulated.

II. *S. australiensis* McL. (Treadwell, Fiji and Samoa).

1. *Tentacles only jointed near ends and only  $\frac{3}{4}$  the length of the palps.*
2. *Very small accessory teeth, on one side only of the plates.*
3. *End piece of dorsal cirrus distinct, short.*
4. Shafts of compound setæ not denticulated.

III. *S. (Dorvillea) crassa* Chamberlin (Mem. Mus. Comp. Zool. Harvard College, 1919).

1. Tentacles with numerous joints, and same length as palps.
2. *Maxillæ all simple hooks.*
3. No terminal piece to dorsal cirrus.
4. *Shafts of compound setæ denticulated.*

**B. Three rows of maxillary teeth on each side.**

IV. *S. moniloceras* Moore ("Polychæta from Monterey Bay and San Diego, California," Proc. Acad. Nat. Sci. Philadelphia, 1909).

1. *Tentacles 6-8 joints. Palps half again as long, and both only  $1\frac{1}{2}$  times as long as prostomium.*
2. *Maxillæ of inner series with teeth on one side only, some with two equal terminal teeth.*
3. *Conical "style" at end of dorsal cirrus.*
4. *Shafts of compound setæ finely denticulated.*

**C. Four series of toothed plates on each side.**

V. *S. rubra* Grube & Treadwell (West Indian Leodicidæ).

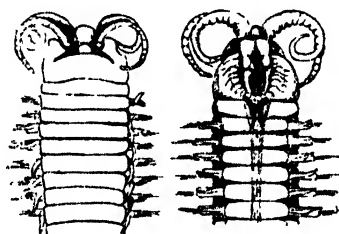
1. *Palps longer than tentacles. Tentacles with 9 articulations.*
2. Maxillæ of outer row pinnate, inner with teeth on one side only.
3. End piece of dorsal cirrus indistinctly separated.
4. *Shafts of compound setæ denticulated.*

But for the possession of two accessory rows of denticles on each side in the jaw apparatus, *S. rubra* would be hardly separable as a distinct species from *S. gardineri*.

The collection contains two specimens, one from the Maldives (Hulule Male Atoll, Statn. 4), the other from the shore of Pungutiayu Islet, off Wasin, East Africa. Both are well preserved, but the former was killed with the head well extended (text-fig. 112). In the latter it is contracted, so that the nuchal papilla is not well seen until the peristomial border is drawn back, and the tentacles and palps are shortened. Notes on this specimen while alive are useful, however, in showing that the nuchal pits were not so slit-like in life. the rough sketch made showing them much like Treadwell's figure of the living *S. rubra*. "Lively in its movements. Body round, slightly flattened underneath; pink with thin red lines intersegmentally. Tentacles (not palps) annulated. Dorsal cirri large, simple, and almost colourless."

The rough sketch referred to above shows the pro- and peristomia and their tentacles and palps in about the proportions of Gardiner's preserved specimen. They are shorter than this in

Text-figure 112.



*Staurocephalus gardineri*, sp. n.—Dorsal and ventral views of anterior end of the Maldivan specimen.  $\times 4\frac{1}{2}$ .

In the former note nuchal organ and recesses; in the latter the large mouth, in front of which the ventral edge of the prostomium appears as a small knob.

spirit; the flattening of the ventral surface seems to have been exaggerated by preservation, though it does not exceed that of other species described.

The specimens are 1.3 and 2.7 mm. wide without the feet, with the feet 2.5 mm. and 4.0 mm. for the East African and Maldivan respectively. The setae project nearly as far beyond the feet as the feet do from the body. Both examples are regenerating the tail end; the Maldivan measures 50 mm. in length with 100 segments, the East African has 30 before the new part begins.

The large tapering dorsal cirri are conspicuous, recalling those of *Oenone*; the first foot bears one of fair size, thus differing from that of most other species.

The form of the body, as usual in allied species, is peculiarly truncated anteriorly (see text-fig. 112), the widest part being but a few segments behind the peristomium, which is but little

narrower than this; behind this point the body tapers gradually to the tail.

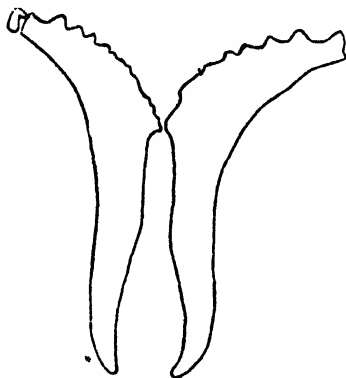
In section the body is remarkably arched dorsally and flattened to a creeping sole ventrally, the feet arising from the edge of the flattened part, *i. e.* far below the middle line of the side.

The segments are short and sharply marked off from one another. In the contracted East African specimen this applies to all but the first few; in the Maldivan the second ring of the peristomium (which is as distinctly marked off from the first as are any of the setigerous segments from one another) and the next four segments are about eight times as broad as long. They then gradually lengthen, over most of the body being six times as broad as long. Towards the posterior regenerating part the proportion returns to eight or more.

The dorsal skin is marked by fine longitudinal wrinkles.

No anal cirri can be made out.

Text-figure 113.



*S. gardineri*.—Lower jaw (it is not symmetrical).  $\times 25$ .

The prostomium is remarkably flattened from side to side, deep dorso-ventrally. (Its proportions and relations to the peristomium are best shown by the figures of the dorsal and ventral aspects of the anterior end.) In this it resembles the descriptions of the other four species given above (especially see Chamberlin's account of his *D. crassa*), but no detailed figure of this remarkable *ensemble* has yet appeared. (Ehlers' figure of *S. cerasina* in "Mag. u. Chil. Strandes" is not unlike this species in the ventral view, but the dorsal is quite different.)

The main features of the jaw apparatus are:—

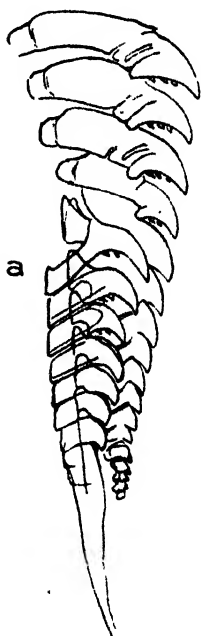
- (1) Lower jaw (text-figure 113) densely black, and showing no separation into component plates except for a nodule or two at each distal horn. The teeth are roundly pointed and well separated, not broad-ended and close together as in the set of species to which *e. g.* *S. similis* below, belongs.

- (2) About 30 pairs of toothed plates in the upper jaws on each side, i. e. 120 parts in all.
- (3) There is no fusion of the proximal plates, which are however joined together vertebra fashion (text-fig. 114 a).
- (4) Inner row composed of flat triangular but curved teeth, with long brown supports. In a side view they appear as slender brown prongs. They have three small denticles on either side of the base of the main point (text-fig. 114 b).

Text-figure 114.



Text-figure 116.



Text-figure 115.



The three figures together make up practically the whole of one double row of teeth.

114. Posterior end. a, point corresponding in fig. 116; b, single tooth of inner row seen from above.
115. Anterior end of the row.
116. Middle part of outer row, isolated.

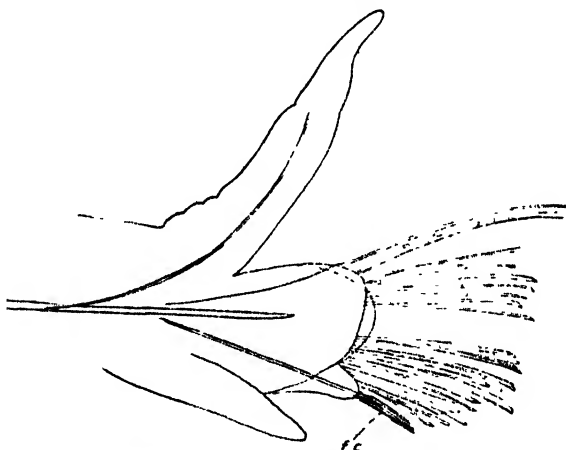
- (5) Outer row composed of more slender curved prongs (short in comparison to e. g. *S. similis*), with complicated double supports and 3 to 5 denticles on one side only. These do not spring from the edge of the plate (text-fig. 116).

The figures (114-116) given suffice for other details including the variations shown in different parts of the ribbon, but it should be noted that, as the teeth point upwards from the plane of the paper, they are not so thick in proportion to length as shown in the drawings.

Figures 114 and 115 together show the whole ribbon with the exception of about six pairs of teeth from the centre. The resemblance of these plates to those of the two main rows in *Staurocephalus rubra* Grube described by Treadwell, and between the lower jaws of the two species, is striking.

The feet (text-fig. 117) are round in section, but somewhat expanded distally by the lips of the seta-sac, which form a wide vertical slit from which the long setæ project in a regular fan.

Text-figure 117.



*S. gardineri*, sp. n.—20th foot showing unjointed cirrus, wide seta-sac, and three kinds of setæ. *f.c.*, fine and narrow-ended compound setæ.  $\times 26$ .

The dorsal cirrus is long, thick below, gradually passing to a point. There is no end-joint; at most possible traces of articulation may be made out under a low power of the microscope. In this the species differs from the great majority, resembling only *S. crassa* and *S. rubra*. It is supported by the usual single, very slender, and apparently flexible acicula\*, which extends from the centre of the foot to near the tip of the cirrus. The foot itself is supported by a single stout yellowish acicula of ordinary pattern.

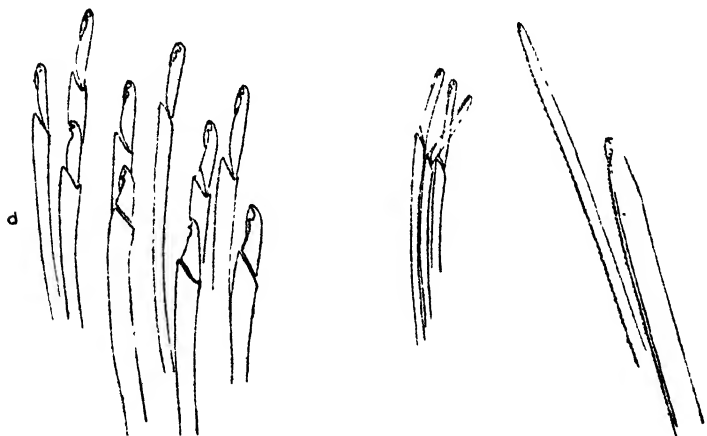
\* Treadwell states that the cirrus contains a tuft of setæ in *S. australiensis* and in *S. vittata*. In the former case his figure suggests one only, as is clearly shown in the 'Challenger' figure. All other species have one only.

The setæ, as usual, consist of:—

- (1) Dorsal slender, colourless, and slightly curved simple setæ. As in several other species, these are finely denticulated along the convex edge and end in one or two very minute hooks. Some are exceptionally fine and transparent. No forked setæ occur.
- (2) A larger ventral bundle of compound setæ resembling those of the genus *Bunice*. In this species they are fairly stout, end-pieces with the usual two teeth and guard of moderate length. Both shafts and ends are smooth.

Text-fig. 118 shows a group of compound setæ in the positions they occupy in the foot, and it is notable that they tend to lie in pairs, more slender shafts and longer-headed setæ projecting

Text-figure 118.



*S. gardineri*.—From left to right:—(1) Group of ordinary compound setæ; (2) part of the ventral group of fine compounds; (3) two of the capillaries, d.e., dorsal and ventral sides of the group.

(1) and (2) are  $\times 200$ . (3) is  $\times 300$ .

further, those with thicker shafts and shorter heads being a little shorter, and both forms tend to broaden towards the ventral side of the foot.

- (3) A small bundle of shorter, finer, and more transparent compound setæ with strikingly narrow end-pieces forming the ventral boundary of the fan. These have not been observed in other species and are not always present, or may be represented by only two or three examples.

All three types are illustrated in text-fig. 118, in which the dorsal side of the group is to the left. To the right is a group of the smaller long-headed compounds to the same magnification as the larger ( $\times 200$ ), but the two capillary setæ, it should be noted, are drawn on the scale,  $\times 300$ .

**STAUROCEPHALUS (DORVILLEA) SIMILIS** \*, sp. n.

Small, up to about 1 mm. in breadth including feet; body arched and broadest anteriorly, uniform in breadth to near tail. Tentacles and palps short, the former with five joints in young specimens, thirteen in older; the latter, like the dorsal cirri, with the usual terminal joint.

Eyes two pairs, the anterior more than twice the size of the posterior.

Lower jaws slender, deeply cut into broad-ended teeth. Upper in two rows on each side, distally both long, slender and curved, more proximally the outer row becomes broader and shorter, eventually fusing into toothed plates; both bear long sharp denticles.

Feet long and cylindrical, dorsal cirri longer than the feet.

No forked setæ, compound with both short and moderately long ends. Simple, not hooked at ends.

Four specimens were obtained among washings from coral collected near the entrance to the docks at Suez, among a large number of other worms, principally *Eunice antennata*. All are small, 4 to 5 mm. long, 0·27 mm. wide, or with the feet 0·4 mm. There are 30–35 segments.

Also ten larger specimens from "washings 7." The largest of these are distended with sexual products, and measure a millimetre in width including the feet, with a length of 17 mm. containing 50 segments. Another worm, with 70 segments, is the shorter, and differs from others in the shortness of its segments and crowding of the feet, which are usually well separated.

Of these specimens two are of so different appearance owing to their narrow elongated bodies and widely separated, freely projecting feet, that only a thorough examination proved their identity. One of them measures 12 mm. in length, 0·4 across the body (0·75 including the feet), and consists of 45 segments.

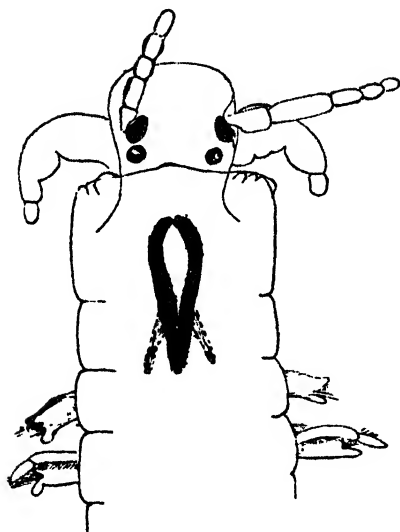
Body broadest just behind the head, flattening and tapering gradually to the tail. Highly arched dorsally, so that the bases of the feet are not visible from above. This is especially the case from the peristomium to the fourth or fifth setigerous segment, which region is somewhat distended to accommodate the musculature of the dental apparatus which extends far behind the plates themselves. This distension goes so far as to partially obliterate the intersegmental groove dorsally, in the smaller specimens entirely. Anal cirri four, two being long and jointed, two very short.

Seen from above the prostomium appears flat †, but it is really deep dorsoventrally and narrower below as in the preceding

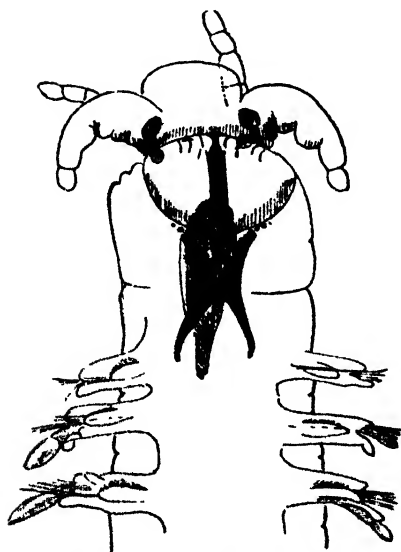
\* *I. e.* not markedly differentiated from several other species.

† In two specimens the front is depressed into a funnel which I take to be an artifact.

Text-figure 119.



Text-figure 120.



*S. similis*, sp. n.—Dorsal and ventral views of a specimen made transparent in glycerine.  $\times 95$ .



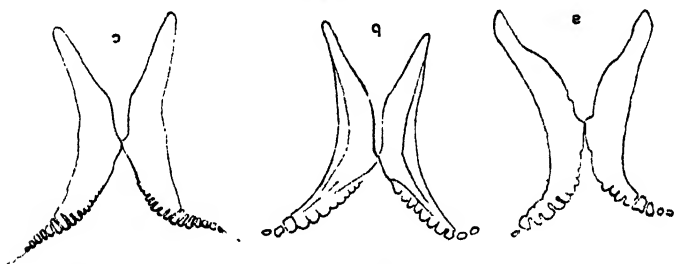
species. (This is not shown in text-figs. 119 and 120 as they were drawn from a transparent specimen.) It also narrows to a neck passing within the high collar of the peristomium.

It bears jointed tentacles, 5 joints in the young, up to 13 in the older, and broad flattened palps, which terminate in the usual conical joint. The former arise from depressions near the large oval anterior eyes, the latter ventrally as usual. The smaller brown posterior eyes seem to consist of a globular retina and small lens, structures not made out in the larger anterior pair.

The mouth is wide but nearly closed by two large lateral lips formed from the peristomium.

These structures are illustrated by text-figs. 119 and 120, dorsal and ventral views of the anterior end of a small specimen soaked in glycerine but *not* compressed by a cover-slip. Both show the positions of the dental plates; in the latter the mandibles are

Text-figure 121.



*S. similis*.—Lower jaw-plates of three specimens. Note (1) asymmetry, (2) greater separation of distal plates in largest specimen.

*a* & *b*  $\times 136$ , *c*  $\times 90$ .

almost as clear as if dissected out. Their conspicuousness in spirit specimens is noted above as characteristic of all these small Staurocephalids. The same figures show the structure and proportions of the feet, which, owing to their ventral origin, are best seen in text-fig. 120, in which the ventral and dorsal cirri (the latter shaded), lips of seta-sac and its papilla, and relative lengths of the setæ are shown.

The lower jaw of the first specimen dissected (text-fig. 121*a*) shows remarkably slender cutting parts, more deeply cut up than in, e.g., *S. longicornis* or *S. pallidus*. A second specimen, however, was more normal, as shown in text-fig. 121*b*; but in both the jaws are light and particularly distinctly toothed. The deep separation of the teeth in text-fig. 121*a* suggests young plates in which the constituent parts are not yet fully fused up; but the blackness of the shafts indicates greater age than that of the other specimen, in which the lateral areas indicated are brown, not

black. The worms from which they were taken are of nearly the same size.

The third sketch (121 c), drawn to a lesser scale, shows the

Text-figure 122.



Text-figure 123.



*S. similis*.—One double row of toothed plates.  $\times 280$ . For lettering, see text.

Details of same:—(a) Posterior plate in this case not so completely fused as in fig. 122. For other lettering see text.  $\times 300$  except *d* (from a large specimen) which is  $\times 200$ .

lower jaw of one of the larger specimens, which is less completely fused than even the smaller, though the plates are completely

black throughout. The range of individual variation is therefore considerable.

The jaw apparatus consists of two rows of plates on either side, the general arrangement of which is shown in text-fig. 122. Of these, the inner row begins some distance posteriorly to the outer as a toothed plate—*a* in text-fig. 122, which anteriorly articulates with the proximal of a series of more or less triangular toothed plates bearing denticles. At *b* the outer row begins as a series of similar triangular denticulated plates. Both series now approximate in size and shape so that at *c* they are only distinguishable by the length of the second denticle in teeth of the inner row, both being long curved teeth, finally at the end losing their denticles and becoming soft.

In plan this is like the apparatus of *S. vittata* described by Treadwell from the West Indies, but the details differ. It is impossible to make out details, especially of the middle region in the row mounted whole, but they were obtained from other specimens in which the plates were separated. Text-fig. 123 shows a variation

Text-figure 124.



*S. similis*.—6th foot (of one of the elongated specimens)  
seen from above.  $\times 95$ .

of the proximal plate in which its origin by the fusion of distinct elements is visible, and the first rudimentary plates of the outer row are also shown. The detailed shape of a plate of the outer row is shown at *a*, and also in text-fig. 123 *b*. Text-fig. 123 *c* and *d* shows the rapid approximation in shape between outer and inner plates in the middle of the row.

The articulations of these plates and attachment to basal membrane are complicated.

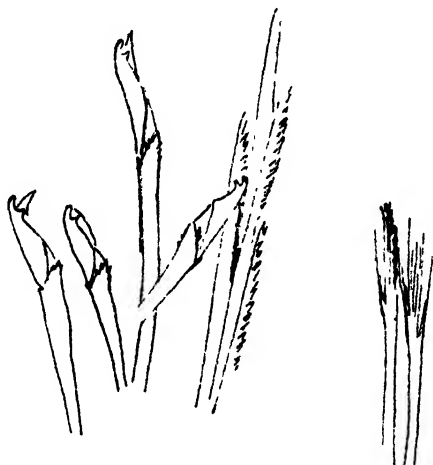
The long plates of the inner row have a toe and heel attachment of which the long toe part, in a side view, may strongly resemble a third row of simple teeth without denticles.

This fusion of the proximal plates shows the evolution of the tooth plates of other Eunicidæ. It has gone still further in *S. melanops* described by Treadwell, *l. c.*

A foot is shown in text-fig. 124, whilst text-fig. 125 shows a group of setæ from the 15th foot of one of the smaller specimens, four capillaries and four out of the seven compound setæ being present. Of the former the longest is so delicate that no details

could be made out at a magnification of  $\times 600$ , but it appears to be one which in other feet is seen in side view as a simple smooth capillary of extreme slenderness and fine point. In another example a similar seta was found to be finely denticulated. Of the other three, two have dilated tips with sharp serrations, in the third the tip, though serrated in the same way, appears to be slender. In other specimens these serrations show a tendency to split away forming a brush-like end to the setæ, as shown to the right of text-fig. 125. This is certainly an effect of breakage and wear and may correspond with the fact that in these specimens a good many of the compound setæ have lost their end pieces, but it does indicate an internal structure which may be

Text-figure 125.



(Group of setæ from 15th foot of smaller specimen; to right, a pair of brush-like setæ.  $\times 600$ .)

the rudiment of the forked setæ so characteristic of certain species.

The denticulations of the shafts of the compound setæ just below and also above the angle of the joint and occasional projection of the hood are notable features, more prominent in some specimens than in others of the same size and, as would be expected, more developed in the larger specimens. In these also fine toothing of the guard can be made out, which is not visible in the young examples, as in text-fig. 126. The simple setæ are similar, but more numerous; the delicate broad ends sometimes show rudiments of hooks, scarcely however in many cases distinguishable from the ordinary serrations.

Text-figure 126.

*S. similis*.—Setæ of a larger specimen.  $\times 600$ .**STAUROCEPHALUS (DORVILLEA) RUBROVITTATUS Grube.**

This well known species was found in nodules of *Lithothamnium* dredged in 3 to 5 fathoms in St. Vincent Harbour, when several specimens were obtained. Curiously, it did not occur again, even in the numerous washings from similar material from adjacent localities. It appears to differ slightly in colour from European examples, as the brilliant crimson bands occupied most of the dorsal surface, broad and less definite alternating with clear intersegmental lines. The underside, tentacles, palps and feet, and posterior parts of the prostomium were colourless as usual.

2. On the Family *Linguatulidæ*. By MARY L. HETT, B.Sc., F.Z.S. (late Professor of Biology, Lady Hardinge Medical College, Delhi).

[Received October 2, 1923 : Read February 5, 1924.]

(Text-figures 1-13.)

In the following paper an attempt has been made to give a short general account of the anatomy and life-history of the family Linguatulidæ. In so far as they are accessible, all important works of previous writers on the subject have been consulted, and the account has been compiled from the data thus obtained, together with the result of a number of independent observations. The scope of the paper was originally intended to include a systematic review of the genera and species belonging to the family, but, owing to the publication of Dr. Sambon's recent work on the subject in the *Journal Trop. Med.* (78), I have rewritten that part of my article, provisionally adopting Dr. Sambon's classification, but adding additional notes and information.

The material on which my own investigations were made is as follows :—

1. About 200 specimens obtained from animals dying in the Gardens of the Zoological Society, London.

2. Specimens in the collections of

- a. British Museum (Natural History), S. Kensington, S.W.
- b. Royal College of Surgeons, Lincoln's Inn Fields.
- c. University Museum of Zoology, Oxford.
- d. University Museum of Zoology, Cambridge.
- e. Indian Museum, Calcutta.
- f. Museum of Zoological Dept., University College, London.

3. Specimens received from Professor J. P. Hill, Professor Ashworth, Professor Leiper, Dr. W. N. F. Woodland, Dr. E. A. Fraser, Dr. Pixell-Goodrich, and Col. Walker, Principal of the Veterinary College, Lahore, to all of whom my thanks are due.

4. Specimens obtained from snakes and lizards in India.

In addition to the examination of external features, a number of these specimens were dissected, while others were investigated by means of serial sections—the sections including both larval and mature forms.

My thanks are further due to Dr. H. Marrett Tims for his help in the earlier stages of the work : to the authorities of the above museums, through whose kindness I have been able to

examine the collections in their charge; and to the authorities of the Zoological Society for material obtained from animals dying in the Society's Gardens.

### HISTORICAL.

In 1789 Frölich (27) gave the name *Linguatula serrata* to a tongue-worm from the body-cavity of a rabbit.

In 1811 Humboldt (44) described another species of tongue-worm from the rattlesnake with the name *Porocephalus crotali*. This same species was redescribed by Rudolphi eight years later (76) as *Pentastoma proboscideum*. Rudolphi's name has been widely used, although the other generic names undoubtedly have the priority. Leuckart employed it in 1860 (53), dividing it into two subgenera: 1. *Linguatula* and 2. *Pentastomum* (s. str.) with the following diagnoses:—

Subgen. *Linguatula* Frölich.

Body flattened, raised dorsally, with a crenated margin. The body-cavity extends into the lateral portion of the rings. (Transl.)

Subgen. *Pentastomum* Rudolphi.

Body cylindrical. Body-cavity continuous. (Transl.)

In 1883 Hoyle (43) declared these to be of generic rank, and added the following characterization to Leuckart's diagnosis:—

*Linguatula*: hook-glands diffuse; opening of œsophagus into the anterior termination of the intestine; testis double; vesicula seminalis single.

*Pentastomum*: hook-gland in two masses; œsophagus opens on the inferior surface of the intestine; testis unpaired; vesiculæ seminales seem to be double in most cases.

Lohrmann in 1889 (56) pointed out that the differences in the form of the hook-glands, position of the œsophageal aperture, and the lateral prolongations of the body-cavity were not of sufficient importance to constitute generic distinctions. Stiles in 1891 (90) agreed with Lohrmann, and further remarked that it still remained to be proved whether the testis is single in all species of *Pentastomum* (s. str.). Stiles recognized the priority of the name *Porocephalus* over that of *Pentastomum*, but proposed to retain the latter because of its widespread use. In 1898, Shipley (84), while acknowledging the force of the criticisms put forward by Stiles and Lohrmann, still regarded the distinctions between *Linguatula* and *Pentastomum* (= *Porocephalus*) as of sufficient importance to establish their generic rank.

In 1899 Ward (96) described a new genus of Linguatulids, with the name *Reighardia*, for *Pentastoma lari* Megnin. He gave a very scanty diagnosis, which was later amplified by Vaney and Sambon (93).

In 1910 Vaney and Sambon (93) described a new genus, to which they gave the name *Raillietiella*. It was distinguished from the foregoing genera by the possession of protuberances round the hook-pits, the anterior position of the female genital pore, and the bifid posterior extremity. In 1915 I was able to investigate the anatomy of a species of this genus. The result of my observations showed further considerable differences in the internal anatomy of the female reproductive system:

Quite recently Dr. Sambon (78) has published a complete systematic review of the family, and has added a number of new genera to those mentioned above.

Most of the works in the Bibliography at the end of this paper deal with individual species only. Apart from Dr. Sambon's paper, the more important of those which attempt to give some general idea of the group are as follows:—

Diesing in 1835 (22) gave descriptions of about two dozen species. Leuckart in 1860 in his historic Monograph (53) gave a detailed account of the anatomy and development of *Linguatula serrata*, with plates. He also added a list of the then known species of the family with original Latin diagnoses, but unaccompanied by figures, except of the hooks. Stiles in 1891 (90) supplied a bibliography complete to the date of publication, and Shipley in 1898 (84) gave a short account of the group.

#### Family LINGUATULIDÆ.

Internal, vermiform parasites with flattened or cylindrical annulated bodies; the rings vary in number throughout the family, but are more or less constant for each species. The anterior end of the body is known as the cephalothorax or head, the remainder as the abdomen; the two divisions have usually no clear line of demarcation, but they may be separated by a distinct neck. The mouth, guarded by a chitinous framework, is anterior in position; the anus posterior; both are either terminal or subterminal. On either side of the mouth are a pair of protractile chitinous hooks which serve as organs of attachment. The body is provided with a cuticle which bears one or more rows of apertures on each segment, known as "stigmata" or external openings of the epidermal glands. The sexes are distinct, the females being considerably larger than the males. The ovary is unpaired; fertilization is internal, and the first stages of development take place within the uterus. The testes are paired or unpaired. The male genital aperture lies in the mid-ventral line a short distance behind the mouth. The female genital aperture is either at the posterior end of the body, a short distance in front of the anus, or else anterior, in the same relative position as the male genital pore. There are several well-marked glandular masses whose ducts open on the cephalothorax. The muscles are striate except in certain parts in the male reproductive system. There are no special circulatory or respiratory



organs. The nervous system is simple, consisting of a sub-oesophageal ganglion with a circum-oesophageal ring and a series of paired nerves arising from the ganglion.

The embryos possess two (or three) pairs of clawed limbs which disappear completely during development, and at the same time a secondary annulation appears which has no reference to the original segmentation of the body. The life-history is usually carried out in two hosts, but there is reason to believe that in some cases an intermediate host may be absent. The larval stage occurs in many Vertebrates, especially Mammals. The adult forms live chiefly in the lungs, air-passages, and body-cavities of Reptiles, though some are found in Birds and Mammals.

## CUTICLE.

## GENERAL ANATOMY.

The whole body is enclosed in a relatively thick chitinous sheath, which is continued into the stomodaeum, rectum, reproductive apertures, gland-ducts, and hook-pits. This cuticle is secreted by the layer of columnar epidermal cells lying immediately below. The chitinous sheath is divided by a series of circular constrictions into a number of rings; these rings are observable in all the species I have examined; they are sometimes difficult to trace in adult specimens of *Sebekini* (where they are very numerous), and in most mature females they become more or less obliterated owing to the great distension of the uterus. Where the superficial annulation is not clearly visible, the rings may often be traced by the circular band of muscle-fibres which is closely applied to the centre of each annulus on its inner surface and by the arrangement of the stigmata (*v. sub.*). Although they do not represent the original segmentation of the body, the number of these rings has been regarded as absolutely diagnostic of a species. They are no doubt of great value in systematic work, since the number is generally more or less constant for each species; but it is impossible to depend on this feature alone, for the following reasons: (1) as mentioned above, the rings are sometimes obliterated in mature individuals, especially females; (2) a certain number of rings may disappear at the anterior or posterior end during metamorphosis; (3) the body may contract in such a way as to produce wrinkles which are difficult to distinguish from annuli.

The cuticle is pierced in places by a series of minute tubes, leading from certain glands to the exterior. The small circular pores by which these glands open to the outer surface are known as "stigmata"\*. In the earlier stages they occur in rows, but later on this arrangement is obscured, especially where the pores are numerous, and they appear to be scattered irregularly over the surface. As a rule the stigmata are concentrated towards the centre of each ring. The relative size and number of the

\* *Vide* p. 115, footnote.

openings vary in the different species. They are numerous in *Sebekini* and *Porocephalini*, 5 to 10 irregular rows being found on each segment, except in the case of *Porocephalus* spp., where there are only two or three rows. In *Linguatulini* and *Raillietellinæ* there is only a single row in the centre of each annulus.

The presence of a spinous or denticulated posterior border in each ring is a characteristic larval feature. It has been described in the larval forms of *Linguatula serrata*, *Porocephalus kachugensis*, *Pentastoma heterodontis*, *P. najæ-sputatrix*, *P. gracile*, and *Sebekia oxycephala*. I have verified this statement with regard to most of the species mentioned above, and in addition have noticed the occurrence of small chitinous spines in the same situation in *Armillifer armillatus* and larval specimens from *Lates microlepis* (probably = *Leiperia cincinnalis*). Leuckart (53) states that these spines are thrown off during the last ecdysis in *Linguatula serrata*; and this phenomenon is probably of general occurrence, since the spines are found in fully-formed larvæ of the species mentioned above, but do not appear in the adults.

Histologically the cuticle on the surface of the body can be divided into two layers: (1) a very thin, darkly-staining layer; (2) a thicker, slightly-staining layer with a lamellar structure. This distinction holds good also for the cuticle lining the various apertures, except for that of the buccal cavity and hook-pits, where the cuticle has different staining properties.

#### Original Observations.

Several stains were employed to demonstrate the different layers, with the following results:—

Hæmatoxylin and Orange G....	Surface of body :
	(a) Outer layer, dark purple.
	(b) Inner layer, light purple.
" " " ...	Hook-pits and buccal cavity :
	red brown.
Hæmatoxylin and Picro-Indigo- Carmine.	Surface of body :
	(a) Outer layer, dark purple.
	(b) Inner layer, light purple.
" " "	Hook-pits and buccal cavity :
	purple - blue, green, and yellow.

The three colours in the last case seem to be due to difference in penetrating power of the re-agents, not to differences in the chitin.

In some places the two layers visible on the outer surface of the body appeared to be present in the mouth and hook-pits in addition to the layer mentioned above. In all cases the cuticle of the outer surface is continuous with the inturned portions lining the various cavities. The chitin of the hooks is continuous with that of the hook-pits and has similar staining properties.

In the alimentary canal the distinctive staining of the mouth-cavity gradually disappears in the pharyngeal region, the chitin of the œsophagus staining as on the outer surface of the body. The cuticle of the outer surface of the body was also stained with :—

- (a) Hæmatoxylin only.
- (b) Iron Hæmatoxylin and Picro-Indigo-Carmine.
- (c) Carbol-Fuchsin.

In each case the thin outer darkly-staining layer and a thicker pale inner layer could be clearly seen ; it was specially evident with carbol-fuchsin. Picro-indigo-carmine had very little effect.

### Hooks.

One of the most characteristic features of the group is the possession by the adult of two pairs of sharply-curved chitinous hooklets lying on either side of the mouth. Each hooklet is enclosed in a sac, from which it can be protruded by strong muscles attached to its base. There is considerable range of movement, with consequent alteration in relative position of hooks and mouth. The neglect of this fact has, I think, given rise to conflicting statements in the description of certain species of *Porocephalinæ*. I have observed an actively moving *Porocephalus crotali* alternately protruding and retracting its hooklets like the claws of a cat. At one moment a line drawn through the base of the hooks would have shown the contour of a downwardly-bent bow, at the next a straight line, and lastly that of an upwardly-curved bow. Under these circumstances any statement as to the relative position of hooks and mouth must be treated with caution.

Each hook consists of (1) a curved projecting portion, and (2) a jointed basal portion embedded in the sac, to which the muscles are attached. Both parts are composed of chitin.

### Hook-sacs.

There is a pair of sacs or pits on either side of the mouth. These sacs are elongated in an antero-posterior direction and lined with epidermis and cuticle continuous with that covering the surface of the body. At the base of the sac the cuticle is reflected back, and becomes continuous with the chitin of the hook. A number of longitudinal muscles radiate out from the walls of the sac, and at the anterior end there is also a transverse band of muscles extending from the hook-sacs across the head dorsal to the mouth. This extensive system of muscles allows considerable movements of the hook-pits and hooks, as already described.

### Hooks.

The distal portion of the hook is more or less strongly curved and sharply pointed ; the lower end of this portion widens to form a plate which is expanded dorso-ventrally, but strongly

compressed laterally. This plate is articulated to the basal portion of the hook, which in its turn is attached to the dorsal wall of the sac, and frequently has a strong tooth-like projection for the attachment of muscles.

Sections through the lower region of the curved portion show (1) a thickish outer layer of chitin, (2) a layer of epidermis, (3) a core of loose connective tissue and fibres. Layers (1) and (2) are continuous with the corresponding layers in the hook-sacs. In the upper third of the curved portion there is a second mass inside the first, marked off by a second layer of epidermis and fibres and enclosing a mass of non-cellular material, apparently fat.

The chitin is interesting histologically, as with certain stains it gives a different reaction to that of other parts of the body. As mentioned above, it does not stain readily with hæmatoxylin, but is deeply stained by Orange G and Picro-indigo-carmin.

Small accessory hooks or spines attached to the outer side of the main hooks are of frequent occurrence in larval forms, and are occasionally found in the adult. Complete observations on this point are wanting, but there is sufficient data to support the theory that they are always present at some stage of larval development, but are usually thrown off at the last ecdysis.

Accessory spines or hooks have been observed in the following immature forms:—

<i>Linguatula serrata</i> ...	Both prs. of hooks: Leuckart (53) <i>et alii</i> .
<i>Porocephalus clavatus</i>	Outer pair of hooks only: Stiles (90).
<i>Pentastoma crocidura</i>	Both pairs of hooks: Parona (70).
<i>P. heterodontis</i> ....	" " Leuckart (53).
<i>P. naja-sputatrix</i> ...	" " Leuckart (53).
<i>P. gracilis</i> .....	" " Diesing (22, 23).
<i>Sebekia wedli</i> .....	" " Wedl (97).
<i>S. oxycephala</i> .....	" " Leuckart (53) <i>et alii</i> .
<i>Raillietiella furcocerca</i>	" " Diesing (22, 23).
<i>Armillifer armillatus</i>	Inner pair of hooks only: Hett.
(?) <i>Leiperia cincinnalis</i>	Both prs. of hooks: Sambon (78) & Hett.

There is only one genus known at present in which accessory spines are present in the adult, viz., *Porocephalus* Humboldt.

It will be seen from the above table that double hooks have been observed in species belonging to all the sections of Linguatulidæ, and further investigations may demonstrate their presence in all larval forms. They are least conspicuous in Porocephalini.

#### ALIMENTARY CANAL.

The alimentary canal consists of the following divisions:—

- a. Mouth-cavity.
- b. Pharynx.
- c. Oesophagus.
- d. Stomach or intestine.
- e. Rectum.

a. *Mouth*.—The cuticle which covers the body extends into the mouth-cavity, reaching beyond it as far as the entrance to the intestine. Round the mouth-aperture the cuticle forms a well-marked ridge, which, in the early stages of development, is horse-shoe-shaped (incomplete anteriorly), but finally, in the adult, completely encircles the mouth. In the *Sebekini*, however, it appears to remain incomplete at the anterior extremity throughout life (*cf.* Sambon, 78). The ridge may be circular, oval, pear-shaped, or transverse, but the shape is usually constant for any one genus. The chitinous armature is perhaps most marked in the genus *Raillietiella*, where the mouth is nearly terminal; in most other genera it is subterminal.

Within the ridge there is a chitinous projection called by Lohrmann the "mouth-papilla," by Hoyle the "oral papilla, probably protrusible," but declared by Stiles to be a non-protrusible upper lip. Examination of this papilla by means of whole mounts cleared in xylol and by sections shows it to be a solid chitinous mass filling most of the space enclosed by the above-mentioned ring. The mouth-aperture is in this way reduced to a narrow semicircular slit between the posterior edge of the papilla and the ridge. The oral papilla together with the pharynx acts as a suctorial organ, and the whole apparatus is controlled by a series of strong muscles stretching from these organs to the body-wall.

b. *Pharynx*.—The pharynx is crescent-shaped in transverse section, and lined with very thick, deeply-staining cuticle. The horns of the crescent at the anterior end of the pharynx point dorsally, but farther back they bend round and point towards the ventral side. At its posterior end the pharynx becomes triangular or circular in section, and then passes into the oesophagus.

c. *Oesophagus*.—The oesophagus has a relatively small lumen, either dorso-ventrally compressed or circular in section, and lined by a thin layer of lightly-staining cuticle. External to the cuticle of both pharynx and oesophagus is (1) a layer of columnar epithelium, (2) a layer of rather irregular muscle-fibres arranged in a more or less circular manner. In *Linguatulini* the oesophagus opens to the anterior end of the intestine; in *Porocephalini* on the ventral side. Hoyle (43) regarded this as a generic distinction. In *Raillietiellini* the oesophagus opens ventrally. I have not been able to investigate the condition in *Sebekini*.

d. *Intestine*.—The intestine is a long cylindrical tube stretching throughout the greater part of the body. It is straight in all *Linguatulids* so far observed except in the *Sebekini*, where it is stated to be sinuous (*cf.* Sambon, 78). The intestine is lined by columnar epithelium. Outside this is a *membrana propria* and then two layers of muscle: (a) circular, (b) longitudinal. The lining epithelium may be thrown into folds as in *Porocephalini*, or may be produced into finger-like processes as in *Raillietiella* (37), but in either case it is very glandular, and the gut lumen is filled with excretory granules together with broken-down blood-

cells and similar *débris*. Posteriorly the tube narrows and passes into the rectum.

e. *Rectum*.—Histologically the wall of the rectum resembles that of the intestine, except that it is lined with chitin. In most genera it is very short, but in *Raillietiella* it forms a definite narrow tube. Where the anus and vagina open to a common pit, the aperture is transverse or crescentic.

#### SECRETORY SYSTEM.

This consists of:—

1. Epidermal glands, opening to the surface of the body by "stigmata."
2. Head glands, in the region of the cephalothorax.
3. Lateral glands, in the abdominal region.
4. Parietal glands, lining the body-wall.
5. Small glands connected with the alimentary canal and the reproductive organs.

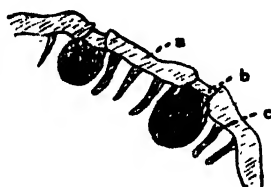
Spencer (88) groups these glands into two classes:—

- A. Epidermal glands, of ectodermal origin.
- B. The remaining glands (2-5 above), of mesodermal origin.

#### *Epidermal Glands.* (Text-fig. 1.)

These glands consist of specialized epidermal cells opening to the surface of the body through small pores or "stigmata"\*. In development the stigmata first appear dorsally, but eventually they are present the whole way round the body, forming more or

Text-figure 1.



Epidermal glands.

a. Cuticle.      b. Gland.      c. Epidermal cells.

less regular rows in each segment. In the adult, however, the rows frequently become irregular and difficult to trace. They are usually confined to the central part of each annulus, but in some cases are scattered over the whole surface of the body. Parona (70) describes a system of anastomosing tubules

\* The term "stigmata" was applied to these apertures before their true nature was understood, and the term is still retained by most zoologists.

connecting the stigmata in a larval *Porocephalus* (*P. crocidura*); this does not occur in any of the species I have examined.

The glands are saccular and of the simple multicellular type, consisting of small groups of columnar epidermal cells sunk a little below the general level and giving rise to some secretion, which takes a deep stain. The neck of the gland passes through the cuticle and opens to the surface by a circular aperture supported by a chitinous ridge. In longitudinal section the glands are flask-shaped, the wall consisting of a single layer of elongated cells with distinct nuclei; the secretion is shed to the cavity of the gland and passes to the exterior through the narrow neck. This neck is non-cellular and consists of a short tube formed by the inturning of the cuticle. The cuticle is thickened around the edge of the external opening, thus rendering the circular pore easily distinguishable.

#### *Mesodermal Glands.*

The cells of the mesodermal glands appear to be of a similar histological structure throughout. They vary considerably in size however, some reaching a diameter of 0.28 mm., while some are relatively small. Stiles has described the larger cells as paler staining than the smaller ones in *Porocephalus clavatus*, but this difference has not been observed in other species. The nucleus is in all cases large and deeply staining, but the outline is frequently indistinct.

The nomenclature of the mesodermal glands is in some confusion, owing to the fact that they have been named according to the position of their ducts, a relation which appears to vary throughout the family. In all cases there are present: (1) a glandular mass in the head, (2) a pair of glands lying on either side of the alimentary canal, (3) a number of gland cells lining the body-wall. In some Linguatulids the limits of these glands cannot be clearly defined. I propose to name them according to their position in the body:—

1. Head glands.
2. Lateral glands.
3. Parietal glands.

Below is appended a reference table showing the nomenclature of other authors:—

	<i>Head Glands.</i>	<i>Lateral Glands.</i>	<i>Parietal Glands.</i>
Leuckart.....	... ..	Hook gland.	Parietal glands.
Stiles .....	Hook gland.	Head gland.	" "
Hoyle .....	.....	Hook gland.	" "
Lohrmann .....	.....	Hook gland.	" "
Spencer .....	Head gland.	Hook gland.	" "

The name "hook gland" was applied by all writers to the gland whose ducts open in the hook-bay, but the relation of these ducts to the glands in question is not constant: *e. g.*, in Stiles's (90) specimens the ducts of the glandular mass in the

head region opened to the hook-bays, while in Spencer's (88) observations the ducts of the lateral glands opened in that region. Therefore it seems advisable to abolish the term "hook gland" altogether.

In *Raillietiella* the glands are not so extensive as in the other groups, and the limits of the different glands are not so clearly defined.

#### *Head Glands.*

These head glands fill most of the head region, and extend backwards to the commencement of the intestine. I have investigated the histological structure in young specimens of *Armillifer moniliformis* and *A. armillatus*. The component cells are rather small and deeply staining; they are not distinguishable in appearance from those of the parietal gland mentioned below.

At the extreme anterior end they form a central mass, but farther back the cells become confined mainly to the peripheral region, owing to the presence of hooks and mouth. Near the entrance of the œsophagus to the intestine the lateral glands appear internal to the head glands, which nearly surround them. From this point the head glands decrease in size posteriorly, and finally terminate over the anterior end of the intestine. It was not possible to determine the limits of the head and parietal glands respectively; they appeared to be confluent.

Each head gland had a central duct; anteriorly each duct branched into two, one branch opening to each hook-bay. Posteriorly the duct disappeared in the substance of the gland.

A similar arrangement of ducts is described by Stiles (90) for *Porocephalus clavatus*. Lohrmann (56), however, describes the ducts of the head gland as opening to the primary sensory papillæ in *Linguatula serrata* and (?) *Sebekia oxycephala*, while Spencer (88) in *Waddycephalus teretiusculus* could find no separate duct for the head glands, nor could he trace any connection between the cells of this gland and the ducts of the lateral glands.

#### *Lateral Glands.*

These are two conspicuous glandular masses lying one on either side of the intestine and extending backwards from the mouth region almost to the posterior end of the body. In *Raillietiella*, however, the lateral glands appeared to be represented by a mass which surrounds the anterior end of the intestine and reproductive organs but does not extend posteriorly through the body.

In *Porocephalus clavatus*, Stiles (90) described the outer cells of the gland as large and pale-staining, the inner cells as smaller, more deeply staining, and similar to those of the parietal glands. In *Waddycephalus teretiusculus*, Spencer (88) says they vary in size; they are similar to those of the other glands, but not so large as the parietal cells. In my sections of *Armillifer armillatus* and *A. moniliformis* the cells are very large and similarly staining. In *Raillietiella* the cells of what I take to



represent the lateral glands are smaller than those of the head or parietal glands.

In *A. armillatus* and *A. moniliformis* each lateral gland has a main duct which divides into two or three branches in the substance of the gland. Anteriorly the main duct runs forward and opens on the sensory papilla over the inner hook-pit. Stiles describes a similar condition in *Porocephalus claratus*, only there the duct opens *below* the papilla. In *Waddycephalus teretiusculus*, Spencer found that the ducts of the lateral glands opened to the hook-bays. In *Raillietiella* the ducts could not be traced. There

Text-figure 2.



Cells from lateral gland.

a. Section of main duct.      b. Radiating canals.

is also a series of very fine chitinous tubes which run from the substance of the gland to the main duct. At the distal end these fine tubes communicate with a clear space bordered by two or more gland-cells, and in the cytoplasm of the cells are fine radiating lines which converge to the central space. This arrangement was first described by Spencer in *Waddycephalus teretiusculus*. The tubes and radiating lines were very clear in my sections of *Armillifer*, but I could not find any trace of them in *Raillietiella* (text-fig. 2).

#### *Parietal Glands.*

These are fairly small-celled glands lining the body-wall and usually more conspicuous at the centre of each annulus. Stiles says they are divided into three areas, one dorsal and two ventral. This appears to be the general arrangement for *Porocephalinae*: I found it so in some serial sections of *Armillifer armillatus*. Here the glands extended throughout the whole body region posterior to the mouth, the cells forming a single or double row between the circular and longitudinal muscles of the body-wall. There was no definite limit between the parietal and head glands, and the cells of the two glands were similar in appearance.

#### *Smaller Glands surrounding*

- a. Oesophagus.
- b. Rectum.
- c. Genital organs.

a. *Œsophagus*.—According to Stiles (90) there are two glandular masses surrounding the œsophagus. The cells are smaller than those of the parietal glands and very pale-staining. I have observed these glands in young *Armillifer moniliformis* and *A. armillatus*; here the cells were very small but rather deeply staining.

b. *Rectum*.—Stiles and others mention glands surrounding the rectum. The former notes that they are small-celled and very pale-staining.

c. *Genital Organs*.—According to Stiles there are no glands in the female round the spermathecæ during the larval stages, but they are present in the adult, and the cells are indistinguishable from those of the parietal glands. These glands were not visible in any of my sections; possibly the specimens were too young.

In the male, Stiles describes a thick layer of large gland-cells "outside the vasa deferentia; the ejaculatory ducts are surrounded by peculiar striated longitudinal muscles which look almost like gland-cells in section." These muscles were very noticeable in young *Armillifer armillatus* and *A. moniliformis* not only round the ejaculatory ducts, but also surrounding the vasa deferentia. The gland-cells were not present in this region.

From a study of the mesodermal glands in various species of Linguatulids, it appears that they have a similar nature and origin in all cases, but have become locally specialized. Their function is unknown, but Spencer (88) considers that they probably secrete a fluid which prevents coagulation of the blood taken into the alimentary canal from the host.

#### MUSCULAR SYSTEM.

All the muscles of the body are distinctly striped except in some portions of the male reproductive system. They may be divided into 5 groups:—

1. Muscles of the body-wall.
2. Muscles connected with the hook-pits.
3. Muscles connected with the oral papilla and pharynx.
4. Muscles of the œsophagus and intestine.
5. Muscles of the reproductive system.

##### 1. *Muscles of the body-wall.*

Posterior to the head region they are arranged as follows:—

a. *Circular Muscles*.—There is a thin layer of circular muscle-fibres immediately below the cells of the epidermis. According to Spencer (88) this layer thins out at two points on the lateral wall in *Waddycephalus teretiusculus*, thus producing the appearance externally of a dark "lateral line." This line has not so far been noticed in any other species. In my sections of *Armillifer armillatus* and *A. moniliformis* there was no noticeable thinning of the muscles at these points.

b. *Longitudinal Muscles*.—Below the circular muscles there is a sheet of longitudinal fibres which is considerably thicker than the overlying layer. In *Waddycephalus teretiusculus* it was of a fairly uniform thickness and formed a continuous sheet (Spencer). In *Porocephalus clavatus* etc. the sheet was incomplete ventrally (Stiles). In *Armillifer armillatus* and *A. moniformis* also that layer is wanting in the mid-ventral line, but is much thickened on either side of it. This gives the dark mid-ventral line noted for these species.

In *Waddycephalus teretiusculus* the two muscle-layers were in close contiguity (Spencer). In *Porocephalus protelis* (= *Armillifer armillatus*) and *A. moniformis* the space between the two layers is very noticeable, and is occupied by the parietal gland-cells.

c. *Oblique Muscles*.—These fibres pass obliquely across the œlom from the dorso-lateral region of the body-wall to a point near the mid-ventral line, thus dividing the body-cavity into a central and two lateral chambers. In *Linguatula serrata* there are two sets of fibres in each segment, one set running downwards and forwards, the other downwards and backwards (Leuckart, 53). A similar condition was found in *Porocephalus clavatus*. In *Waddycephalus teretiusculus* there were two series, but they both pass in a dorso-ventral direction and do not cross (Spencer, 63). In *Porocephalus protelis* (= *Armillifer armillatus*), Hoyle (43) described one series only. In *Armillifer armillatus* and *A. moniformis* it was difficult to see if there were one or two series in each annulus, but it was quite clear that all the fibres ran in a dorso-ventral direction and did not cross.

#### 2-5. Other muscles of the body.

There is a series of strong muscles connected with the hooks, hook-pits, oral papilla, and pharynx. The hooks serve as organs of attachment to the tissues of the host, and, as mentioned above, are freely protrusible and capable of considerable range of movement. A detailed account of these muscles together with those connected with the alimentary and reproductive systems is given by Spencer (88, pp. 10-15, *q. v.*).

### NERVOUS SYSTEM.

This consists of:—

1. A large bilobed subœsophageal ganglion.
2. A dorsal commissure.
3. A series of paired nerves given off from the ganglion.

The *ganglion* is large and very definitely bilobed. From it a dorsal commissure encircles the œsophagus shortly before the entrance of the latter to the intestine.

There are nine pairs of nerves arising from the ganglion, of which the largest is a pair of cords stretching nearly to the posterior end of the body on either side of the mid-ventral line

and just anterior to the longitudinal muscles. The remaining pairs are distributed to the other organs of the body, but their actual course is a little difficult to make out. Stiles (90) and Spencer (88) have both given detailed accounts of its distribution, but their descriptions differ on minor points. This may be due to the fact that Spencer's observations were made on *Waddycephalus teretiusculus* and Stiles's on *Porocephalus clavatus*. I have examined sections of *Armillifer moniliformis*, *A. armillatus*, and *Raillietiella boulengeri*. The preparations were not sufficiently good to show the exact course of the smaller nerves, but there is no doubt that the general plan of arrangement is the same in all these species. Harley (35) and Macalister (58) described a dorsal instead of a ventral ganglion, but this was evidently an error. Several authors have described the commissure as double: Spencer suggests that these observers were misled by the fact that the first pair of nerves are united for a portion of their course just anterior to the commissure, thus giving it the appearance of a double nerve collar.

#### SENSE ORGANS.

There is a pair of conspicuous sensory papillæ on the antero-ventral surface of the head. There are also a number of smaller papillæ, called by Spencer (88) "secondary papillæ."

The pair of primary sensory papillæ is situated in front of the mouth and hooks, but their position varies a little in different genera. Among the Sebekini these papillæ lie at the extreme anterior border of the cephalothorax, frequently giving it a truncated appearance. In *Porocephalus* and in *Armillifer* they are closely approximated on the ventral side of the cephalothorax, and form a kind of bilobed structure immediately above and between the inner hook-pits. In *Kiricephalus* and *Waddycephalus* they are small, rounded projections separated by a definite space and lying one immediately above each inner hook-pit. In *Linguatulini* they lie nearer to the anterior border of the head. In *Raillietiella* the relation is not easy to determine, but they probably correspond to the pair of conspicuous "antenniform papillæ" on the dorso-lateral aspect of the cephalothorax (text-fig. 3).

The investigation of these papillæ is often attended with difficulty because of the great individual variation: in some specimens the papillæ are very conspicuous, while in others they can hardly be detected with a powerful lens.

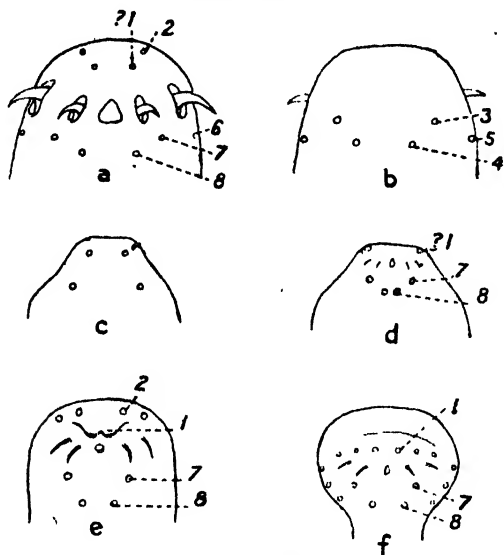
Stiles (90) and Spencer (88) describes seven pairs of secondary papillæ. The latter classifies them as:—

- a. Three dorsal pairs,
- b. Two lateral pairs,
- c. Two ventral pairs,

numbered consecutively 2-8, the primary sensory papillæ being regarded as the first pair.

On examination of a number of Linguatulids, I found that the secondary papillæ also are often extremely difficult to detect; they seem to be more conspicuous in *W. teretiusculus* (described by Spencer) than in most other members of the family (text-fig. 3, *a, b*). The arrangement of the dorsal and lateral papillæ is not constant throughout the family. In *Armillifer* and *Porocephalus* there are two pairs along the anterior border of the head and sometimes several lateral pairs (text-fig. 3, *e*). In *Kiricephalus*, I have been able in a few cases to make out a series of papillæ lying over the

Text-figure 3.



## Sensory papillæ.

- a. Waddycephalus* (ventral). After Spencer.
- b. " (dorsal). " "*
- c. Linguatula* (dorsal).
- d. " (ventral).*
- e. Armillifer and Porocephalus* (ventral).
- f. Kiricephalus* (ventral).

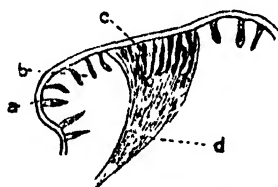
hook-pits and on the lateral aspect of the cephalothorax, but in many instances both these and the ventral papillæ could not be seen. Probably the disappearance of papillæ in this genus is correlated with the habit of burying its head deeply in the lung-wall of the host (text-fig. 3, *f*). In Raillietiellini and Sebekini secondary papillæ have not so far been described, but this may be due to the usually small size of these parasites. The papillæ marked 7 and 8 in Spencer's figure were found in almost every instance, the 7th a short way behind the outer hooks, the 8th a

little posterior to the 7th and more median in position. They do not appear to bear any constant relation to the annulations.

Each primary papilla consists of a little globular mass of modified epidermal cells, supplied by a small nerve from the ganglion. These cells are elongated and stain more deeply than the surrounding cells of the epidermis, but in the species I have examined there is no hollow organ with projecting rods, as described by Stiles.

Stiles was unable to detect sense organs in the secondary papillæ of *Porocephalus clavatus*. Spencer, however, described and figured groups of sensory cells from some of the secondary papillæ of *Waddycephalus teretiusculus*; he was unable to detect them in all the secondary papillæ, but thought they were probably present in all cases. On examining some serial sections of *Armillifer armillatus*, I discovered at the extreme anterior end a little group of sensory cells which corresponded to one of the secondary papillæ on the antero-dorsal region of the cephalothorax. These sensory cells could be traced on four consecutive

Text-figure 4.



Section through secondary sensory papilla.

- |                     |                   |
|---------------------|-------------------|
| a. Cuticle.         | c. Sensory cells. |
| b. Epidermal cells. | d. Nerve-fibres.  |

sections, which also showed the structure of the primary sensory papillæ. These latter were towards the centre of the sections, and the small secondary papillæ were situated laterally. The sensory cells of the secondary papilla resembled those of the primary papilla; they were elongated and curved, and possessed distinct nuclei. The outer ends were in contact with the cuticle, but did not project through it; the inner ends were in connection with a nerve whose subsequent course could not be traced (text-fig. 4). A careful examination of the series of sections failed to reveal groups of sensory cells corresponding to the other secondary papillæ; but this is not remarkable, since the papillæ are very small and the cells are not recognizable unless cut in longitudinal section.

In addition to these sensory papillæ, Stiles mentions a varying number of "inconstant papillæ" on the lateral edges of the flattened anterior end of the body of *Porocephalus clavatus*. These are in all probability not sensory, but possibly aid in locomotion (*v. sub.*, p. 133).

## REPRODUCTIVE ORGANS.

The female reproductive organs consist of an unpaired ovary, paired oviducts, paired spermathecae, and a large uterus frequently spirally coiled and opening to the exterior on the ventral surface.

The male reproductive organs consist of paired or unpaired testes, and vesiculæ seminales, paired vasa deferentia, and cirri, the latter enclosed in a muscular sheath. As a rule, ejaculatory ducts are present.

*Female Reproductive Organs.*

The ovary is unpaired and lies dorsal to the gut, extending from the anterior end of the intestine to the rectum. There is a central lumen, on either side of which the ova form a lateral projecting mass. In *Armillifer grandis* the ovary divides anteriorly into two branches, but this has not been noted elsewhere, though it probably occurs in other species of *Armillifer* also\*.

The paired oviducts pass off from the anterior end of the ovary and encircle the intestine, opening below to the uterus. In the genus *Raillietiella* I have only been able to discover a single functional oviduct; sometimes on the right side, but usually on the left. A careful examination of sections, however, leads me to believe that the ducts are originally paired, but that only one becomes functional, the other undergoing considerable degeneration. In all other Linguatulids that I have examined the oviducts are paired.

A pair of spermathecae are situated on either side, close to the entrance of the oviducts to the uterus, and communicate with the latter by a pair of short ducts. Usually the two spermathecae are of equal size, but in *Kiricephalus pattoni* this is not the case. Patton and Cragg (71) figured the left spermatheca of this Linguatulid as larger than the right, while in two specimens that I have dissected the right is decidedly larger than the left.

The uterus passes backwards from the oviducts, and in an adult is crowded with eggs in all stages of development. In *Porocephalinæ* it is a relatively narrow duct considerably coiled, which may lie entirely ventral to the gut as in *Armillifer*, or may twine around it as in *Linguatula* spp., where the gut is completely hidden by the coils. The terminal section of the uterus is straight and sometimes much dilated when full of embryos; it narrows at the extreme posterior end just before its opening to the exterior.

In *Raillietiella* spp. there is a much simpler and apparently more primitive arrangement. The narrow anterior end of the uterus opens into a long sac with a wide lumen, which extends backwards and forwards ventral to the gut. The posterior

\* v. Haffner has recently made the same observation for *Armillifer armillatus* Wyman (84, p. 163).

portion reaches about three-quarters of the length of the intestine, where it ends blindly. The anterior portion gradually narrows, and eventually forms a duct, opening to the exterior just behind the second pair of hooks.

The *female genital aperture* is median and ventral, and in all genera except *Raillietiella* and *Reighardia* (where it is anterior) the opening is a short distance in front of the anus. The anus and female genital aperture may open to a common transverse pit or they may open separately. In the latter case the genital aperture is crescentic in shape, and may be found about  $\frac{1}{2}$  mm. in front of the anus (e.g., *Armillifer armillatus*) or separated from it by a distance of several segments (8 in *Waddycephalus teretiusculus*). When there is a common pit, the uterus opens to it immediately in front of the anus. Sometimes in specimens where the two apertures are separate but close together, contraction of the intestine takes place on death, and thus forms an artificial pit to which both tubes open conjointly. In *Raillietiella* and *Reighardia*, as before mentioned, the female genital aperture is *anterior*, being situated on the segment behind that which bears the second pair of hooks, in the same relative position as the male genital aperture.

The whole course of the oviducts and the uterus is lined by thin cuticle.

#### *Male Reproductive Organs.*

The *testis* is single in all species except those belonging to the genus *Linguatula*, where it is stated to be double. The lumen is somewhat irregular, and it has been suggested by Stiles (88) that the testis shows an incipient paired condition, evidenced by a pair of folds which project on opposite sides to the central lumen. Lohrmann (56) regards it as physiologically double, since it opens to the vesiculæ seminales by two orifices. In all cases the testis lies dorsal to the gut, stretching from near the anus to about the middle of the body. Anteriorly the testis opens to a paired or unpaired vesicula seminalis. The shape and position of the vesicula seminalis vary a little. In most Porocephalinæ it is single at its commencement, and then divides into two branches which run forwards and downwards, alongside the intestine. In *Raillietiella* the vesicula seminalis appears to be single, and lies entirely dorsal to the gut.

The *vesiculæ seminales* open anteriorly to the paired vasa deferentia, and at the point of junction are given off ejaculatory ducts which vary in length and extend backwards alongside the intestine.

The *vasa deferentia* are ventral in position and run forwards to the middle line, where they unite to form a small median chamber. Communicating with the vasa deferentia in this region are three sacs on each side:—

1. *Cirrus bulb*, which represents an outpushing of the wall of the vas deferens.



2. *Muscular bulb or dilator rod sac*, a very muscular organ containing a chitinous rod, which forms part of the copulatory apparatus, but whose function is uncertain. It was originally described as a "dilator-rod," owing to its supposed activity in dilating the female genital aperture, but later writers have regarded it as a means of retracting the penis after coition. The muscular bulb is also formed as an outgrowth of the wall of the vas deferens.

3. *Cirrus sac*, which constitutes an outpushing of the wall of the median chamber and contains the coiled cirrus.

The paired cirri are in most cases long and coiled, the length being necessitated by the position of the female genital aperture, which is far removed from the spermathecae. In *Raillietiella*, however, where the female genital aperture is anterior and close to the spermathecae, the male copulatory apparatus is somewhat modified; the cirrus is relatively much shorter and the cirrus sac smaller (37).

The male genital aperture is in all cases anterior, opening in the mid-ventral line behind the second pair of hooks. The aperture is usually guarded by three papillae—two lateral and one anterior.

The ejaculatory ducts, vas deferentia, and copulatory apparatus are lined with cuticle, which becomes enormously thick near the genital aperture.

### FERTILISATION.

As pointed out by several authors, impregnation takes place at an early period while the uterus of the female is still a more or less straight tube. At the time of metamorphosis male and female individuals are of approximately the same size, and coition must take place long before the female has attained full dimensions. (Cf. 78, Dr. Sambon's illustration of "*Armillifer armillatus*, male and female in coitu," where the male individual is roughly  $\frac{1}{4}$  the length of the female, whereas the full-grown male of this species is only  $\frac{1}{2}$  the length of the full-grown female.) In this connection it is noteworthy that in several cases where I have found free larvæ emerging from their cysts these individuals have almost invariably been males, although there were many female specimens in the cysts.

According to Lohrmann (56) both cirrus threads are thrust into the vagina and inserted into the spermathecae, where the sperms are deposited. The spermathecae communicate with the uterus by a pair of short ducts, opening just below the entrance of the oviducts. As the eggs pass down through the oviducts from the ovary they are fertilized at the entrance to the uterus. In the uterus they undergo the first stages of development, and give rise to the characteristic embryo with boring apparatus and clawed limbs.

After fertilization the female continues to grow, and in some Linguatulids the growth is so considerable that doubt has been

thrown on the identity of young and fully-grown individuals of the same species.

### LIFE-HISTORY.

In the majority of cases the life-history involves two hosts—an intermediate host which may be a fish or a mammal, and a final host which is usually, but not invariably, a reptile. In *Linguatula* spp. the final host is a mammal, in *Reighardia* a bird, while a mature species of *Raillietiella* has recently been described from the lung of an Amphibian (31).

The adult individuals are found chiefly in the lungs and air-passages of their host, though they may occur in the body-cavity or alimentary canal. In those Linguatulids whose life-history has been observed, it would appear that the eggs pass from the lungs by way of the mouth to the alimentary canal, and thence to the exterior with the fæces. They are then taken up into the alimentary canal of the intermediate host. But it seems possible that the whole life-history is sometimes carried out in one host, the embryos passing from the lungs of the host to the alimentary canal, and from thence by the blood-stream to different organs of the body. When the adult parasite is situated in the lung of the host, eggs are shed to the lung cavity from the uterus of the parent, and in some cases remain in the lining network. Examination of the lung of a snake containing adult female Linguatulids will frequently reveal a number of eggs situated on the inner wall. These eggs pass from the lungs to the exterior through the alimentary canal; they are voided with the fæces, scattered over the vegetation or into the water, and in this way are taken into the alimentary canal of the intermediate host along with the food.

The fact that entrance to the intermediate host takes place in this way has been clearly demonstrated by experiment. Several types of Linguatulid eggs have been used, and, when fed to appropriate hosts, they developed into larvæ which, on the death of the host, were found encysted in various organs of the body.

(a) Leuckart (53) fed eggs of *Linguatula serrata* successfully to rabbits and a goat.

(b) Gurlt also fed eggs of the same species to a goat (mentioned by Leuckart).

(c) Stiles (90) fed eggs of *Porocephalus clavatus*

i. Successfully to mice.

ii. Unsuccessfully to a dog, guinea-pig, rabbit, and dove.

(d) Brodin and Rodhain (14) fed eggs of *Armillifer armillatus*

i. Successfully to *Macacus*, rats, and a young wild cat.

ii. Unsuccessfully to two rats, a cock, a duck, and a jackal.

(e) Neumann (66) found encysted larvæ of *A. armillatus* in two young dogs which had taken their food in a yard where a post-mortem examination had been made of two pythons containing adult specimens of *Armillifer*.

In Egypt and Africa, where larval *A. armillatus* have been found parasitic in natives, it has been suggested that infection was due to the eating of snake's flesh; but that is unlikely, as it does not appear to be a common custom, and certainly most of the other intermediate hosts of *A. armillatus* do not eat the flesh of the final hosts, though infection may occasionally take place in that way.

Unlike the adult parasites, the larvæ of *Porocephalus*, *Armillifer*, *Linguatula*, etc., seem to have little selective instinct as regards particular mammals, but are found in a great variety of Mammalian hosts. In species like *A. armillatus*, for example, the list of intermediate hosts includes representatives of five different orders of Mammals, the greater proportion being Primates or Carnivores. The number of final hosts is much more restricted, and possibly has something to do with the relative size of parasite and host.

Therefore we may assume that for most Linguatulidæ there are normally two hosts: (a) an intermediate host—a mammal or fish; (b) a final host—a mammal, reptile, or bird.

Probably, however, the whole life-cycle can in some cases be carried out in one host:—

1. Stiles (90) found in the lung-tissue of a Boa constrictor containing adult male and female *Porocephalus clavatus* little groups of one to ten eggs with embryos, each group enclosed in a capsule. (This is the only recorded instance of eggs enclosed in a common cyst.) He also found cysts with "small Pentastomids" in the same position, the inference being that the "small Pentastomids" had developed *in situ*. It is difficult to imagine that the eggs were shed to the lung-cavity and developed there without any further migration, because in that case there would be no opportunity for the removal of the egg-envelopes by the gastric juice of the host. Probably the larvæ in the cysts had developed from embryos which had made their way to the stomach, lost their outer covering, and been carried back to the lungs by the blood or lymph streams. There are two other recorded instances of larvæ in the lung-tissues of the definitive host (Jacquart (47) and Wheeler (99a)).

2. Chatin (23) mentions the finding of encysted specimens of what he believed to be *Sebekia oxycephala* in the liver of *Alligator mississippiensis*, which is one of the final hosts for this Linguatulid.

### 3. Original Observations:—

(a) On examining some specimens of Australian Black Snake (*Hoplocephalus superbis*) given to me by Dr. E. A. Fraser, I found a number of small cysts embedded in the outer wall of the lung and apparently containing young Linguatulids; there were adult specimens of *Waddycephalus teretiusculus* present in the lungs and body-cavity. In these cases the embryos probably reached the alimentary canal, and were carried back to the lungs by the

blood-stream. This is the more likely since in the black snake the cysts were all found on the outer wall of the lung.

(b) From the body-cavity of a *Lachesis lanceolatus* which died in the Zoological Society's Gardens, I obtained cysts with one immature female and two immature male Linguatulids (probably *Porocephalus stilesi*).

(c) I have recently examined the following specimens in the collection of the Indian Museum, Calcutta:—

- i. Encysted larvæ (apparently of *Kiricephalus pattoni*) from the mesentery of the Rat-Snake, *Zamenis mucosus*, which is a final host for this parasite.
- ii. An encysted larva of *Raillietiella orientalis* from the body-cavity of *Naia tripulians* (the final host of *R. orientalis*).

Apparently therefore, though the life-history normally involves the presence of two hosts, it may in some instances be carried out in one.

#### *Migration of Embryos.*

When the embryos, still enclosed in the egg-envelope, reach the alimentary canal of the intermediate host, the outer coverings are dissolved by the action of the digestive juices and the embryos set free. By means of a boring apparatus and clawed limbs, the embryo pierces the gut-wall and is carried by the blood- or lymph-stream to some organ of the body, where it becomes encysted and undergoes a series of larval ecdyses, finally emerging from the cyst when larval development is complete. The actual migration has never been observed, and it has been suggested by two authors (Schaeffer (79) and Looss (57)) that two migrations take place, one at a very early stage, one later. Schaeffer bases his argument on the fact that larvæ are frequently found encysted in the serosa of the gut-wall, not in the mucosa. He suggests that the embryos make their way to this point and there become encysted, thus preventing perforation of the gut, and that later they migrate to other organs. Objections to this theory are that

(1) There is no evidence of a second migration.

(2) Larvæ are found in all stages of development both in the intestinal wall and in the other organs of the body. If they migrated first to the intestinal wall and later to the other organs, early stages would occur in the former locality and advanced stages in the latter. But this is not the case: larvæ in all stages are found in all the organs of the body.

(3) Where free larvæ are found they are fully formed:—

#### *I. Experimental Infection.*

(a) In Leuckart's rabbits the larvæ remained encysted till about 7 or 8 months after the eggs had been introduced into the

alimentary canal of the hosts. They then became free in the thoracic and abdominal cavities, causing severe lesions and extravasation of blood.

(b) In Stiles's mice the last animal died  $18\frac{1}{2}$  weeks after infection. All the viscera were riddled with cysts; a few larvæ had emerged and were free in the body-cavity.

In both (a) and (b) the free larvæ had reached their full development.

## II. *Natural Infection.*

### 1. *Recorded Cases.*

In about 80 recorded cases of the occurrence of Linguatulid larvæ in Mammals they were found 10 times free in the abdominal cavity. In the few cases where a description is given they are evidently fully developed.

### 2. *Original Observations.*

In 15 findings of Linguatulid larvæ they were free in the body-cavity 5 times, and in each case they were fully formed.

Further, the position of larvæ in the intermediate host leaves little room for doubt that the embryos are transported by the blood- or lymph-streams to the organ in which they develop:—

#### 1. *Position of larvæ in cases of experimental infection.*

(a) Leuckart (53) fed eggs to rabbits, and after 8 weeks found small nodules in liver and lungs containing young larvæ about 1 mm. long.

(b) Stiles (90) fed a mouse with eggs of *Porocephalus clavatus*. It died after 32 days, and larvæ were found (about the same stage as those of Leuckart after 8 weeks) in liver, lungs, kidneys, and peritoneum.

(c) Brodin and Rodhain (14) fed a young wild cat with eggs of *Armillifer armillatus*. It died after 21 days, and small granules were found in the liver consisting of "more or less modified eggs," in some cases one or two hooks being recognizable.

#### 2. *Position of larvæ in cases of natural infection.*

##### 1. *Recorded Instances.*

(a) Neumann (66) found a young larva in a hepatic vein. It was at an early stage of development, since the hooks were scarcely indicated.

(b) In about 80 recorded cases of the finding of larval Porocephalinæ they occur 40 times in the liver, 30 times in the mesentery, 14 times in the wall of the intestine, 9 times in the lung-wall, 9 times in the peritoneum, 7 times in the mesenterial glands, 6 times in the spleen, once in the kidneys, once in the brain-cavity, 4 times free in the intestine, 10 times free in the body-cavity.

## 2. *Original Observations.*

In 15 cases which I have observed, the larvæ occurred 6 times in the liver, 6 times in the mesentery, 4 times in the wall of the intestine, twice in the lung-wall, once in the mesenterial glands, 5 times free in the body-cavity, once in the kidney.

Thus it will be seen that the cysts are found most often in the liver, but very frequently in the mesentery and less often in the walls of the alimentary canal. The presence of a larva in the hepatic vein suggests that they are carried by the portal vein to the liver and mesentery (where they occur in largest numbers), and may occasionally pass from the liver through the hepatic veins to other organs. Also their presence in mesenterial glands supports the idea of their transportation by the lymph canals. Some may remain in the wall of the intestine and become encysted there. But, though the above methods of migration are probably the most usual ones, the larvæ may occasionally make their way to the abdominal cavity direct through the intestinal wall. Some few also remain in the lumen of the intestine (there are 4 or 5 recorded instances), but this is not of common occurrence.

In many of the observed and recorded cases of Linguatulid infection death was not due, directly at all events, to the action of the parasites. Where it could be definitely attributed to this cause, death occurred either at a very early stage of the infection, or at a late stage when the larvæ were fully developed or nearly so.

The first eventuality is the less usual—it occurs chiefly in cases experimentally infected, where no doubt the infection was abnormally severe and death was probably brought about by the migration of the embryos. I have found one naturally infected case of this kind in a gecko where the liver was riddled with small white granules which I believe to be due to Linguatulid embryos. There was considerable extravasation of blood in the liver tissue, and the infection must have been extremely heavy.

In most of the cases where death is directly attributable to the parasites, the latter are full-grown larvæ or nearly so. Death results from various causes according to the location of the larvæ—pneumonia, peritonitis, etc., and, in cases where the larvæ have begun to emerge, serious lesions ensue. But before death actually occurs, the Mammalian host must be in an enfeebled condition and likely to fall an easy prey to its enemies. If only a few parasites are present, and death to the host does not result, the larvæ become encysted again and die. This occurred in some of Leuckart's experiments, and would account for the occasional finding of cysts in mammals containing calcified remains of Linguatulids.

## *Usual Method of Entrance to the Final Host.*

The larvæ are taken into the mouth of the final host, along with the flesh of the intermediate host in which they occur.

*Experimental evidence.*—Brodin and Rodhain (14) fed larvæ of *Armillifer armillatus* to a *Causus rhombeatus* which was killed 70 days after infection. Four half-grown specimens of *Armillifer* were found in the lung.

Stiles (90) fed larvæ of *Porocephalus clavatus* to *Tropidonotus natrix* and *Pelias berus* (not natural hosts). The experiment was unsuccessful—i. e., the parasites did not become mature, but the larvæ were found in the body-cavity.

These two experiments give proof that the final host *can* be infected in this manner, and it is probably the normal method, since many of the intermediate hosts are known to be the prey of the final hosts.

Free larvæ could make their way at once from the mouth-cavity into the respiratory passages of the snake, but, where the larva is still encysted, it must pass to the stomach before it can be released from its outer coverings. In the latter case the future history of the larvæ is a matter for conjecture. Stiles (90) maintains that they bore their way through the gut into the abdominal cavity, and then through the lung-wall into the lung-cavity. This may be so, but there is no direct evidence as to the latter part of the hypothesis. In Stiles's own experiment the larvæ certainly found their way into the body-cavity, presumably through the gut-wall, and there are many instances of the finding of adult Linguatulids in the body-cavity of snakes, usually attached by their hooks to the intestine. But there is nothing to show that they can make their way from this position to the lung\*. Further, though more frequently found in the air-passages, they are not confined to that region of the body, both immature and full-grown specimens having been found in the abdominal cavity.

### *Metamorphosis.*

When fully developed the larva emerges from the cyst. It then possesses an annulated body, anterior mouth, and two pairs of double hooks. The secretory, alimentary, nervous, and reproductive systems are developed, and differ from those of the adult in little but size. The difference of relative position of male and female genital apertures is clearly visible. The posterior border of each ring projects, and is provided with a row of chitinous structures, forming merely a denticulated edge as in *Pentastomum gracile* Diesing, or a regular circle of small spines as in *Porocephalus kachugensis* Shipley.

On transference to the final host, a further ecdysis takes place, and the animal assumes adult characters. The double hooks are thrown off and replaced by others which are generally single, but

\* Stiles found an adult female specimen of *Porocephalus clavatus* in the body-cavity of *Boa constrictor*, and close to it a hole in the lung-wall, but this hole had apparently served the parasite as a mode of egress from the lung, which contained 22 specimens of the same species of Linguatulid.

may have an accessory spine. The rings then lose their spiny border. Further development consists mainly in increase in size.

In the final host, female specimens as a rule preponderate over the males. Whether embryos of both sexes are produced in equal quantities is hard to say. Leuckart (53) maintained that this was the case, and attributed the lesser number of adult males in *L. serrata* to their smaller size, which would facilitate their expulsion from the nasal cavities of their host by means of sneezing. But this explanation would not hold good for Reptilian hosts. Examination of larvæ in the intermediate host leads me to believe that male and female individuals are produced in approximately equal numbers. In the fully-formed larva, males and females are at first equal in size, but the latter subsequently grow at a much more rapid rate. The males are ultimately about  $\frac{1}{2}$  to  $\frac{2}{3}$  the size of the females. They are much more active, and therefore possibly more easily dislodged by the host. In both sexes the parasites are anchored to the tissue of their host by means of the hooks, but as a rule, at a later stage, the female becomes more firmly attached, the cephalothorax being sunk to a greater or lesser extent in a cavity hollowed out in the lung-wall, and in a few cases (e.g., *Armillifer annulatus* and *Kiricephalus pattoni*) even projecting right through the lung-wall into the body-cavity. Males, however, are never found in a similar situation.

The number of rings in the adult Linguatulid is sometimes less than that in the larva, owing to the obliteration of annuli, especially in the tail region. They can usually be counted with accuracy in the adult male, but are difficult to make out in many females owing to the distension of the body by the embryos.

#### *Method of Locomotion.*

As above mentioned, both female and male individuals are attached to the tissues of their host by means of the two pairs of retractile hooks. In the early stages of the post-larval, free-living period they move actively by worm-like contractions and expansions of the body, these creeping movements being facilitated by the temporary anchorage afforded by the hooks and by the flattened ventral surface of the body. This flattening of the ventral surface (especially towards the anterior end) is found in the males and usually also in the young females of nearly all species. As a further aid to locomotion there are frequently present papillæ and tooth-like projections on the ventral surface. Of this nature are the "inconstant papillæ" described by Stiles (90) in *Porocephalus clavatus*, "scutes" seen on the male of *Armillifer armillatus* by Dr. Sambon (78), and the denticles observed projecting from the angles of the rings of the male in *Armillifer moniliformis* by Heymons (41). The appendages are on the whole more marked in the latter case than in any other species that I have examined. In *Raillietiella* spp. (both male



and female) there is a row of papillæ on each side of the body at the edge of the flattened area; in each row the papillæ occur alternately on the annular and inter-annular regions (text-fig. 5, d). In the adult female the body usually becomes cylindrical owing to the distension of the uterus; a period of comparative inactivity supervenes, during which time the parasite remains firmly anchored by means of the hooks, and the cephalothorax may be partially embedded in the lung-wall of the host.

### Family LINGUATULIDÆ.

#### Subfamily RAILLIETIELLINÆ Sambon.

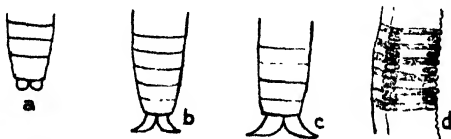
#### Genus RAILLIETIELLA Sambon.

This genus was established by Dr. Sambon in 1910, to include a new species of Linguatulid found by Vaney and Sambon in the peritoneal cavity of *Bitis gabonica* and the trachea of *Bitis arietans*. Three years later three specimens belonging to the same species from the body-cavity of *Zamenis ravigieri* were given to me by Dr. Pixell-Goodrich, and I was able to study their anatomy in detail. The generative organs on the whole are of a simpler structure than those of Porocephalinæ; in the male the vesicula seminalis is unpaired; in the female there is a single functional oviduct, usually on the left side, though occasionally it is found on the right; apparently a pair of oviducts are laid down in the embryo, since traces of the second can usually be seen in sections. The uterus is not coiled, but thin-walled and capable of great distension, occupying the greater part of the body-cavity when filled with developing ova. The vagina opens anteriorly in the corresponding position to that of the male genital aperture.

#### RAILLIETIELLA BOULENGERI Vaney & Sambon, 1910.

The female specimens examined by me were of the same average length as those of Dr. Sambon, but a few were con-

Text-figure 5.



a. Posterior end of *Raillietiella mediterranea*,  $\times 9$ .

b. " " *R. orientalis*,  $\times 9$ .

c. " " *R. boulengeri*,  $\times 9$ .

d. Flattened ventral surface of young ♀ *R. mediterranea*,  $\times 9$ .

siderably longer, one reaching a length of 60 mm. The male specimens were 10 mm. in length, and in both male and female

the average number of rings was 30-40. The lobes of the terminal segment are pointed and sharply curved (text-fig. 5, c).

*Additional hosts:—*

<i>Bitis nasicornis.</i>	{ Specimens obtained from snakes dying in the Zoological Society's Gardens.
<i>Psemmophis sibilans.</i>	
<i>Sepedon hæmachates.</i>	Oxford Museum.

*RAILLIETIELLA FURCOCERCA* Diesing.

Leuckart (53) points out that the original description given by Diesing (22, 23) was apparently based on immature forms. A further consideration of Diesing's remarks on the species makes this almost a certainty:—

1. *Position of the parasite.*—Some were found in the abdominal cavity and mesentery of their hosts, whereas mature forms more usually occur in the air-passages. It is also noteworthy that some of the specimens were taken from *Amphisbæna alba*, while the others occurred in snakes. Possibly those from *Amphisbæna* were of a different species to the rest, since it is unusual to find the same species occurring both in Ophidia and Lacertilia.

2. Diesing remarked that both sexes were of the same size; this statement is obviously erroneous if it refers to fully-grown specimens; if there were actually male and female specimens present of approximately the same size, they must have been immature.

3. Leuckart further states that in Diesing's specimens the hooks were geminate. This is not known to occur in the adults of any other species of *Raillietiella*, but geminate hooks are of frequent occurrence in the immature forms of many Linguatulids; and it is quite possible that, when further observations have been made on the young forms of other species of this genus, the presence of geminate hooks in the early stages will be found to be a constant feature.

*Original Observations.*

I have examined various specimens of *Raillietiella* (all mature females) taken from the lungs of *Boa imperator* and *Coluber melanoleucus*, and have little doubt that they all belong to Diesing's species. The average length is 40 mm., and one specimen reaches a length of 60 mm. The rings are in most cases obliterated, but in three individuals they can be counted, and number 26, 33, and 38 respectively. (Shipley (85) says that Diesing's specimens in the Vienna Museum have "about 40.") The lobes of the terminal segment are acuminate, but less curved than in *R. boulengeri* and *R. orientalis* (text-fig. 6). Therefore the only points of difference between my specimens and those described by Diesing are:—

1. *Length of female*—given by Diesing as 9-13 lines (=19-27 mm.), whereas my specimen measured 40-60 mm.

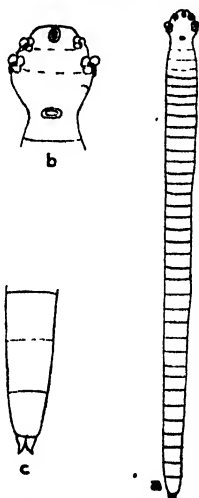
2. *Hooks*—in Diesing's specimens said to be geminate, in mine single. These two differences are easily accounted for on the supposition that Diesing's specimens were immature.

*Hosts*:—

*Boa constrictor*, *Zamenis constrictor*, *Spilotes* sp., *Coluber melanoleucus*, lungs; *Boa imperator*, lungs and body-cavity (new host); *Amphisbæna alba* (?).

Sir A. Shipley (85) mentions specimens of *Raillietiella* found in the lungs of *Varanus exanthematicus ocellatus*, together with

Text-figure 6.



*Raillietiella furcocerca* Diesing.

- a. Adult ♀,  $\times 3$ .      b. Cephalothorax of ♀,  $\times 9$ .  
c. Posterior end of ♀,  $\times 9$ .

(?) *Sambonia lohrmanni* (second finding). There were two parasites, length 21.5 and 9 mm. respectively. The rings could not be counted, but were apparently about 40. It is possible that these are small specimens of *R. boulengeri*, but more probably they belong to a new species allied to *R. geckonis*.

N.B.—Since I wrote the above, Dr. Giglioli (32) has described specimens of *Raillietiella* from *Amphisbæna alba* which he believes to belong to the species *furcocerca*, but his description gives colour to my suggestion of the separate identity of the specimens from this host.

The general characters which he mentions are common to several other species of *Raillietiella*—e. g., *R. boulengeri*, *R. orientalis*, *R. mediterraneus*, etc.; but there are two points which call

for attention, viz.: (1) presence of two small papillæ above the oral shield; (2) size, viz.: length 26 mm., breadth 1 mm.

(1) I have found two small papillæ in a similar position in some examples of *R. boulengeri*, but they are not as a rule very marked; the prominence of these papillæ may well be a specific character peculiar to these parasites from *Amphisbæna*.

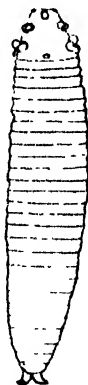
(2) Dr. Giglioli's specimens were apparently mature, but they measure considerably less than those which I have obtained from *Boa imperator* and *Coluber melanoleucus*, and correspond with the length given by Diesing. As mentioned above, the specimens described by Diesing were almost certainly immature, and therefore the length given by him will be less than that of the adult parasite. It is, however, quite possible that Diesing associated two species under the same name, viz.:—(a) One from *Amphisbæna alba*; length of adult female 22–26 mm. (as further described by Dr. Giglioli). (b) One from the other hosts mentioned; length of larva 22–26 mm., length of adult female 40–60 mm. (as described above by me).

I therefore suggest that the name *Raillietiella furcocerca* should be retained for the larger species and that the species from *Amphisbæna alba* should be renamed *R. giglioli*, n. sp.

#### RAILLIETIELLA GECKONIS (Dujardin) Diesing.

I have obtained one specimen from the lung of *Gecko verticillatus* and other specimens from the lung of *Hemidactylus flaviviridis* Rüppell (new host).

Text-figure 7.



*Raillietiella indica* Geddoelst, ♀, × 20.

#### RAILLIETIELLA INDICA Geddoelst. (Text-fig. 7.)

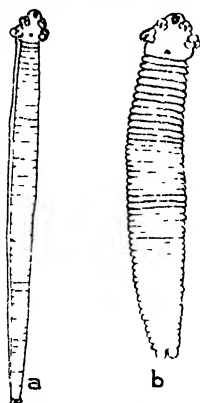
After a careful examination of the type-specimen in the Indian Museum, Calcutta, I am inclined to think that it is an immature female. This species differs from most other members of the

genus in the shape of the cephalothorax. The mouth does not open at the extreme anterior end, but slightly behind it on the ventral side; the dorsal papillæ project from the anterior border of the cephalothorax, giving it a truncated appearance, as noted by Geddoelst (31).

**RAILLIETIELLA MEDITERRANEA Hett. (Text-fig. 8.)**

The body is dark in colour and slender. Length of female 20–35 mm. Length of male 10–15 mm. Number of rings in both sexes 40–50. The posterior bifurcation is not so marked as

Text-figure 8.



*Raillietiella mediterranea* Hett.

a. ♀,  $\times 3$ .      b. ♂,  $\times 9$ .

in some other species of *Raillietiella*; the small posterior protuberances are blunt and rounded instead of flattened, curved, and pointed (text-fig. 5, a).

*Host of adult*:—*Zamenis gemonensis*, lungs and body-cavity.

**RAILLIETIELLA ORIENTALIS Hett.**

Average length of female 34–37 mm., largest specimen 46 mm. Length of males 7–11.5 mm., average length 10 mm. Number of rings in both sexes (text-fig. 5, b) 40 or more.

This species differs from *R. furcocerca* Dies. as follows:—

1. Body is relatively shorter and more slender.
2. Rings more numerous.
3. Habitat: Oriental region.

*Hosts of adult*:—

*Zamenis mucosus*, lungs.

*Naja tripudians*, lungs and trachea.

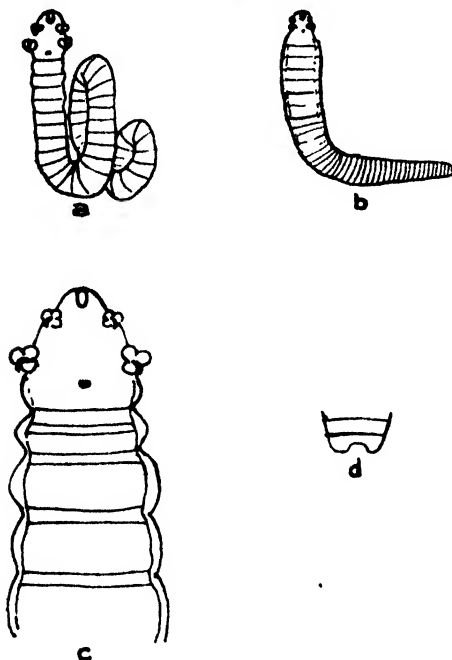
*Host of larva*:—

*Zamenis mucosus*, on intestine.

*RAILLIETIELLA SPIRALIS*, n. sp. (Text-fig. 9.)

In the adult female the posterior part of the body is spirally coiled. It is more or less cylindrical, tapering slightly towards the posterior end, but with a narrow, flattened area on each side of the abdomen. There is a slight narrowing of the body between the cephalothorax and abdomen. Length about 20 mm.; width of cephalothorax 1.5 mm. The length given here is only approxi-

Text-figure 9.

*Raillietiella spiralis*, n. sp.

- a. ♀, × 5.    b. ♂, × 5.    c. Anterior end of ♀, × circ. 12.  
d. Posterior end of ♂, × circ. 12.

mate, as the body is closely coiled and therefore difficult to measure accurately, especially as there has probably been some shrinkage. For the same reason the rings could not be counted with certainty, but there seemed to be about 60.

In the male the body is curved but not coiled; like the female, it is cylindrical, with lateral flattened areas, but the cephalothorax is relatively much smaller, being only about half the width of the anterior end of the abdomen. Length 13 mm., rings 60-70.

In both sexes the mouth lies at the extreme anterior end; the armature is thimble-shaped. The hooks are single and sharply

curved. The dorsal papillæ are conspicuous. The posterior end is bifid, but the projections on either side of the anus are even less marked than in *R. mediterranea*.

This species resembles *Linguatula* spp. in the possession of a bilobed terminal segment and of lateral flattened areas, but here the flattened area is much less marked. It differs from species of *Linguatula* in almost every other particular, whereas it possesses the main distinguishing features of the genus *Raillietiella*, viz.: anterior position of the female genital pore, trapezoidal arrangement of the hooks, terminal mouth, and fleshy protuberances round the hooks (for further details, v. 40).

*Host of adult*:—*Cælopeltis monspessulana*, lungs; Palestine.

Subfamily POROCEPHALINÆ.

Section *SERIKINI* Sambon.

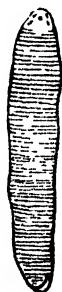
Genus *ALOFIA* Sambon.

*ALOFIA INDICA* v. Linstow. (Text-fig. 10.)

Synonym: *Porocephalus indicus* v. Linstow.

*Description*.—Only females found. Young specimens 20 mm. long, 2 mm. broad. Anterior end of the body thin, then thickened and spindle-shaped; behind this again it contracts to form a neck .79 mm. in diam. The older animals were 24 mm. long, 5 mm. in diameter. Rings on the ventral side at intervals of

Text-figure 10.



*Alofia indica* v. Linstow, ♀,  $\times 2$ .

.44 mm.; lateral edges of rings have posteriorly finger-shaped prolongations, becoming progressively smaller towards the posterior end. Vagina in front of anus. Uterus convoluted. Eggs average .052 mm.  $\times$  .044 mm. (Abridged from v. Linstow, 55.)

This species was discovered in the lungs and trachea of the gharial. I have examined the type-specimens in the Indian Museum, Calcutta, and add the following particulars:—

There was one whole mature female specimen and a number of smaller individuals, apparently immature females; also several broken specimens.

The body was cylindrical but slightly flattened; of approximately the same diameter throughout except at the extreme posterior end, which was tapering, pointed, and sharply incurved. The mouth was rather large, lying midway between the two pairs of hooks, which are in trapezoidal formation. The hooks were single and sharply curved; as far as I could determine they were smooth. The rings were clearly visible the whole way round the body; they were numerous and very difficult to count, but there seemed to be about 60.

The "neck" described by v. Linstow in the immature individuals does not appear to be a constant feature, as some of the young specimens showed no trace of constriction behind the cephalothorax.

This species resembles the figure given by Dr. Sambon of *Alofia ginæ* (78), but differs from it in the presence of a pointed, incurved posterior extremity. *Alofia indica* is also considerably larger than *A. ginæ*.

*Host of adult*:—*Gavialis gangeticus*, lungs and trachea.

#### Section *PROCEPHALINI*.

#### Genus *PROCEPHALUS* Humboldt.

##### *PROCEPHALUS CROTALE* Humboldt.

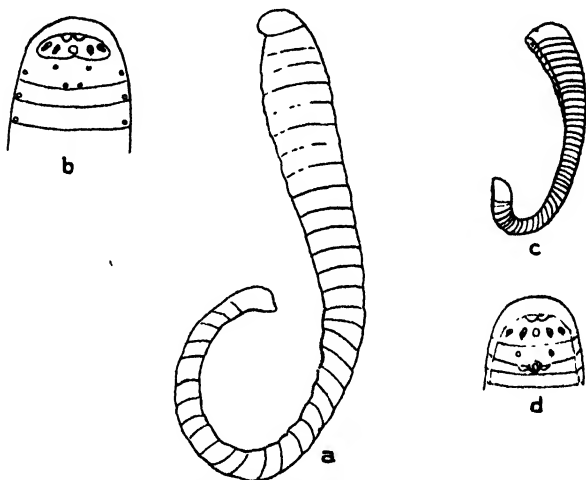
Owing to lack of material there has been some confusion among previous writers in the description of this species. It was first described in 1808 by Humboldt (45), who obtained specimens from *Crotalus cumanensis* (= *C. terrificus* Laur.). He regarded it originally as an *Echinorhynchus*, then as a *Distoma*, but later (44) assigned it to a new genus and species—*Porocephalus crotali* (1811). It was described as *Distoma crotali durissi* by Rudolphi (1809) (75), redescribed as *Polystoma proboscideum* by that author in 1812, and finally renamed by him *Pentastoma proboscideum* (76). Apparently Humboldt adopted this last nomenclature in the 2nd and 3rd editions of 'Ansichten d. Natur' (1826 and 1849).

Diesing (1835 and 1850) described (22 & 23) several allied species under the one name *Pentastomum proboscideum* Rudolphi, including one which does not appear to occur in rattlesnakes but is peculiar to boas, and another found only in *Lachesis* spp. His example was followed by Dujardin (1844) (25), Leuckart (1860) (53), and Leidy (1884) (52). Shipley (1898) (84) restored the name *Porocephalus crotali* Humboldt (priority of the specific name having been previously pointed out by Bell in 1880 (3)), and gave a new figure of the species from *Crotalus*. In 1912 Dr. Sambon (77) maintained that four species had been con-



founded under the one name, and he proposed to retain the appellation *Porocephalus crotali* for the one obtained from the rattlesnake. This species he described as having 80 rings, the number having been stated as such by Diesing (22, 23) in his description of *Pentastomum subcylindricum*, which is the immature stage of *Porocephalus crotali*. Diesing described a number of immature forms under this heading; his figures show a varying number of rings, and in certain cases some of these look more like wrinkles than true annulations. One immature specimen figured from *Tupinamba teguixin* has only 44 rings, and has been regarded by Dr. Sambon as a new species—*P. wardi* (later referred to genus *Sambonia*). Leuckart, who examined about

Text-figure 11.

*Porocephalus crotali* Humboldt.

a. ♀, × 3.

c. ♂, × 3.

b. Cephalothorax of ♀, × 6.

d. Cephalothorax of ♂, × 10.

85 specimens of *Pentastomum subcylindricum* from the viscera of *Didelphys philander* (sent him by Diesing), states definitely (53) that Diesing was in error when he gave the number of rings as 80. According to Leuckart they resembled *Pentastoma proboscideum*—i. e., they possessed "about 40 rings." It is quite likely that the immature forms examined by Leuckart belonged to the species *P. clavatus* Sambon, the adult form of which occurs in boas; but in any case, unless there is some further description in the 2nd and 3rd editions of Humboldt's 'Ansichten d. Natur,' which I have been unable to obtain, the only clear evidence for the existence of a species in the rattlesnake with 80 rings is Diesing's statement with regard to the larval form.

Against this statement are the following facts:—

1. In the original description given by Humboldt the number of rings is not mentioned, but the figure published by him in 1811 (44) shows about 29 or 30. Figures of that date are often inaccurate with regard to such matters of detail, but a drawing which represents only half the actual number of annulations is rather unusual.

2. I have examined specimens from *Crotalus adamanteus*, *C. atrox*, and *C. horridus*, and found that in each case the females had 30–35 rings, the males 32–34. This is slightly less than the average number of rings found in *P. claratus*. Since the number of rings is not constant either in the forms from the rattlesnake nor in those from the boa, I should have doubted whether the slight discrepancy was sufficient to establish a specific distinction had it not been for the fact that there was a further difference in the shape of the body. The specimens from the rattlesnake resembled each other, and differed from specimens from the boa in the possession of a relatively shorter, thicker body, the anterior end being markedly club-shaped. One other small point of difference is the fact that in the species from the boa the dorsal surface of the head, as noted by Dr. Sambon, is “strikingly gibbous.” This did not occur in any of the specimens that I have examined in rattlesnakes, though it is scarcely a specific character.

I think, therefore, that the specimens I have described below from the rattlesnake are identical with the species originally described by Humboldt, and if there exists another species with 80 rings, it must be regarded as specifically distinct.

*Diagnosis* (after Humboldt).—Body cylindrical and club-shaped, yellowish, with milk-white proboscis abruptly truncated and bearing on the ventral surface five brownish retractile spines. Transparent, with transverse wrinkles, whitish at the edge. Longest individuals 62 mm. long; 8 mm. across anterior extremity, 2 mm. across posterior extremity.

*Further description* (specimens obtained from *Crotalus adamanteus*, *C. atrox*, and *C. horridus*) (text-fig. 11):—

*Female*. Length 50–65 mm. (average 60 mm.); breadth across cephalothorax 4.0–8.0 mm.; breadth in front of terminal segment 2.0–3.0 mm. Number of rings 30–35. The cephalothorax is club-shaped and not clearly marked off from the abdomen. The body is cylindrical, flattened ventrally, and incurved at each extremity. The greatest width is across the cephalothorax, and from this point the body tapers gradually towards the posterior end. The terminal segment is enlarged to form a bulb-like swelling with a conical apex. The rings are flat and bear no projecting ridge; they tend to become obliterated towards the anterior end in the adult. The mouth is rather small and oval; it lies a little anterior to the centre of the space enclosed by the inner hooks.

The hooks are sharply curved and the outer pair possess slender accessory spines. The anus and vagina open to a common pit at the extreme tip of the terminal swelling. Stigmata are numerous and appear to be irregularly scattered over the segment.

*Male.* The male resembles the female in general shape, number of rings, etc. The body, however, is straighter and only slightly incurved. Length 25-27 mm.; breadth across cephalothorax 3 mm.

#### Genus KIRICEPHALUS Sambon.

There seems to be considerable range in size of individual females belonging to this genus. The specimens of *K. coarctatus* which I have observed are considerably smaller than those mentioned by Dr. Sambon, and in *K. pattoni* I have found apparently mature female specimens varying from 50-125 mm. in length. The male *Kiricephalus* is from  $\frac{3}{4}$  to  $\frac{1}{2}$  the size of the female.

In this genus the constricted neck of the female seems to be due to mechanical pressure, mature individuals being found with the cephalothorax projecting through the lung-wall of the host. The males remain free in the lung-cavity or merely attached to the lining of the lung by the hooks. They are characterized by a slight narrowing of the body behind the cephalothorax, but there is no definite constriction.

In all three species of this genus the anus and vagina in the female open to a common subterminal crescentic slit.

#### KIRICEPHALUS COARCTATUS Diesing.

*Additional host* :—

*Zamenis flagelliformis* (Testaceous snake).

Dr. Sambon has pointed out (78) that the species described by me in 1915 (38) under the name *Porocephalus globicephalus* is synonymous with that to which he had assigned the name *P. coarctatus* in 1910 (95). I have no doubt that the species are identical, and therefore that the name *P. coarctatus* takes priority. At the time that I wrote the article I had not seen that part of Dr. Sambon's paper which deals with this species. To the best of my recollection, he himself had kindly given me a transcript of the paper in question, which I took to be complete, whereas it actually contained only a part of the original article.

#### KIRICEPHALUS PATTONI Stephens.

It is to be noted that in the figure accompanying Stephens's original description of this species (89) the mouth has been printed with the posterior end uppermost. The male of *K. pattoni* is rather more tapering than the female, with a slight

narrowing behind the cephalothorax. Length 25–37 mm.; number of rings 33.

Up to the present the only known hosts for *K. pattoni* are *Zamensis korros* and *Z. mucosus*. Some little time ago I examined some specimens of *Kiricephalus* from (a) *Python spilotes*, (b) *Lioheterodon madagascariensis*.

(a) From the body-cavity of *Python spilotes*. One mature female, one male. The female specimen was 120 mm. long, but was so swollen out by the contained embryos that the rings could not be counted with any certainty. The male specimen was 30 mm. long; the rings were quite distinct and numbered 33.

(b) From the lungs of *Lioheterodon madagascariensis*. Three mature females, one with the cephalothorax deeply embedded in the lung-wall. Here, too, the annulations were obliterated.

In both these cases the females were indistinguishable in appearance from a typical *K. coarctatus*.

In the case of the specimens from *Python spilotes* the male parasite is of the same size as the male of *K. coarctatus* and has the same number of rings. I think, therefore, that *Python spilotes* must be considered as a new host for the species.

With regard to the specimens from *Lioheterodon madagascariensis* it is impossible to speak with certainty until the number of annulations is known. If these really are specimens of *K. coarctatus*, then *Lioheterodon madagascariensis* is a new host; they may, however, prove to belong to a hitherto undescribed species of the genus. It is not *Pentastomum heterodontis* Leuckart, because, although the rings are largely obliterated in my specimens, I feel sure they are not anything like 58 in number. Further, the stigmata are fairly numerous on each annulus, and not arranged in one row as in *P. heterodontis*.

#### Genus ARMILLIFER Sambon.

##### ARMILLIFER ARMILLATUS Wyman.

The larval forms of *Armillifer armillatus* have attracted considerable attention owing to their frequent occurrence in Man, chiefly in West Africa and Egypt. The first description of the larval *A. armillatus* as a human parasite was published by Pruner in 1847 (72), and since then there have been numerous reports of its occurrence in Africa. From the nature of the case these observations are largely made from the point of view of the human pathologist, and it is sometimes a little difficult to refer the parasite described to its species, especially as some authors have considered *A. armillatus* Wyman to be identical with *A. moniliformis* Diesing. Looss, for example, regarded the difference in the number of rings in these two forms to be merely due to difference in age, suggesting that rings which were present in the

larva became obliterated in the adult (57). This contention cannot be maintained, in view of more recent investigations of the two species in question (cf. Shipley (84), Sambon (78)). I have observed a number of adult specimens of *A. armillatus* from *Python sebae*, *Python regius*, and *Bitis arietans*; and of larval forms from Man, *Cercopithecus mona*, *C. engythithia*, *Perodicticus ibeanus*, *Crossarchus obscurus*, *Hyomoschus aquaticus*, and *Mungo galera*, and have found that, except in a few very immature specimens, it is always possible to distinguish them from *A. moniliformis*. The most characteristic features of demarcation, even in the larval forms, are:—

(1) The number of rings which are clearly demonstrable, viz.:

*A. armillatus*, 20–22 rings in the female.

                  14–17       "       "       male.

*A. moniliformis*, 28–30 rings in both sexes.

(2) The shape of the terminal segment, which is a more or less rounded cone in *A. armillatus*, whereas in *A. moniliformis* it is sharply pointed.

There seems to be considerable diversity of opinion as to the frequency of occurrence in Man. Earlier writers regard it as exceptional, but Seiffert (82, 83, 1910) in 218 post-mortem examinations found 17 cases of infection, while Schäfer (79) in 1912 found 19 cases in 150 examinations.

The method of infection is doubtful; it has been suggested that it came about through the consumption of snake's flesh by the natives, but, as mentioned above, this seems unlikely, and, as pointed out by Seiffert (82), some of the other intermediate hosts (e. g., the giraffe) certainly do not become infected in that way. It seems much more probable that infection takes place through the drinking of infected water.

*Additional hosts* (larval forms):—

*Cephalophus leucogaster*, viscera.

*Potamochoerus penicillatus*, viscera.

*Herpestes urva naso*, liver, mesentery, spleen, and free.

*Hyomoschus aquaticus*, intestine.

*Mungo galero*, liver, mesentery, and lung.

#### ARMILLIFER ANNULATUS Baird.

Some doubt has been expressed as to the position of the vaginal opening in this species. Harley (35) stated that the vaginal aperture was a short distance in front of the anus, but that both apertures open to a single cleft. In two or three specimens of *A. annulatus* which I have examined, this single cleft can be clearly seen on the last segment; it is somewhat crescentic in shape and almost terminal.

**ARMILLIFER (POROCEPHALUS) POMEROYI** Woodland.

Dr. Sambon (78) has considered that the parasites described by Dr. Woodland (101) under this heading are merely specimens of *A. annulatus* in which the neck shows a very marked degree of constriction.

Some years ago my attention was arrested by two specimens of Linguatulidæ in the collection of the British Museum, South Kensington, labelled "*Pent. annulatus* from lungs of *Naja melanoleuca*"; and when Dr. Woodland's paper on *Porocephalus pomeroyi*, n. sp. (1922) appeared, I found that his description of the new species agreed with the notes I had previously made on these specimens in the British Museum. Since then I have had an opportunity of examining several specimens of undoubted *Armillifer annulatus*, and, after a comparison of these with the descriptions and figures given by Baird, Harley, Leuckart, Shipley, Sambon, and Woodland, I have arranged the points of difference between *Armillifer annulatus* and *A. pomeroyi* in tabular form for convenience. Most of these points have been previously noted by Dr. Woodland.

Adult ♀:—	<i>A. annulatus.</i>	<i>A. pomeroyi.</i>
Length	* 80–121 mm.	50–71 mm.
Length of cephalothorax	About 4 mm. (i. e., "combined length of not more than 2 annuli").	About 8 mm. (i. e., combined length of annuli 6–9 incl.).
Breadth of cephalothorax	About half length of cephalothorax.	About equal to length of cephalothorax or a little less.
Length of neck	About 1 mm.	5–7 mm.
Rings on abdomen	28–30 plus terminal segment.	29–31 plus terminal segment.
Shape of rings	With projecting bands about 1 mm. long, separated by constrictions about 1.2 mm. long; 1st ring slightly smaller than succeeding ones.	With projecting bands longer than the constriction, giving it a "moniliform" appearance; 1st ring much larger than succeeding ones.
Terminal segment	? Rounded and more obtuse.	Conical and longer.
Adult ♂:—		
Length	† 15–20 mm.	12 mm.
Number of rings	28–29.	36.

\* Baird's specimen measured 2½ in. (= about 57 mm.), but, as the head remained embedded in the lung, this measurement is useless for purposes of comparison.

† Leuckart (53) gives 15–25 mm., but Harley found two small Linguatulids about 1½ in. (= about 29 mm.) long in the nasal fossa of the same cobra from which his female specimens of *A. annulatus* were obtained, and, on dissecting one, he found it to agree in every respect with v. Beneden's description of a male *Linguatula*. Harley did not consider it to be the male of *A. annulatus* because it was so different in external characters to the larger worm. This sexual dimorphism among the Linguatulidæ is now a well-established fact, and Harley's figures, though not very clear, portray specimens which have the general appearance of males and possess 25 rings.

There is a slight narrowing of the body between the region of the cephalothorax and abdomen in several Linguatulids, but, apart from the species here in dispute, the only members of the family which show a definite "neck" are those belonging to the genus *Kiricephalus*, in which genus there seems no reason to doubt that the constriction is in large measure directly due to mechanical pressure. As noted by several observers, the adult female of *Kiricephalus* normally perforates the lung-wall of its host in such a way that the elastic wall of the lung constricts the body just behind the cephalothorax. I have several times found specimens of *K. pattoni* with the head protruding through the lung-wall into the body-cavity of the host. The same observation was made by Harley (35) with regard to Baird's specimen of *A. annulatus*, but the condition differs in the two species. In *Kiricephalus* spp. the area affected by the constriction is very small; in fact, the body has the appearance of a sausage tightly tied at one point. In *A. annulatus*, and still more in *A. pomeroyi*, the neck is longer and appears as a definite tube with regular outline. Dr. Woodland (102) has recently brought forward evidence of a histological nature to show that in *A. pomeroyi* the constriction is not directly due either to external compression nor to muscular contraction, and, indeed, it is hard to see how a compressed region of this length could be produced merely by pressure of the lung-wall.

#### ARNILLIFER MONILIFORMIS Diesing.

I have examined a number of specimens of *A. moniliformis*, and find that my measurements differ slightly from those of Dr. Sambon (78). There is probably a certain amount of variation in this respect, and I have therefore given below Diesing's original description (22) and the result of my own observations, which are in accord with those of v. Heymons (41).

#### *Original description.* (Transl.)

"Tapering, with moniliform segments. Head thick, rounded anteriorly, flattened; posterior end of body sharply pointed; mouth round and placed behind hook-grooves. Length  $1\frac{1}{2}$  in., 4 lines [= 46.5 mm.]; anterior end 2 lines broad [= 4.2 mm.]; posterior end a little over 1 line broad [= 2.1 mm.]; tail segment  $\frac{1}{2}$  line broad [= .5 mm.]. Twenty clearly marked rings (rings have disappeared at anterior end). Hooks light yellow, single. It differs from *Pentostomum proboscideum* [= *Porocephalus clavatus*] by its moniliform body, lesser number of rings, and mouth below the hook-grooves." [Diesing.]

Diesing described a single female specimen from the lungs of *Python molurus*. His illustration shows about 26 rings, 18 being clearly marked.

*Further description.*

*Female.* Length 58-85 mm. (immature specimens 24-50 mm.); width across cephalothorax 3-4 mm.; number of rings 27-30 (not counting terminal segment).

The rings are usually to a certain extent obliterated towards the anterior end in the adult female. More posteriorly they are strongly marked, and the segments swell out between each groove; they are not always "moniliform," the actual shape depending, as pointed out by Sir A. Shipley (84), on the amount of contraction of the body.

The hooks are rather wide apart, and the circular mouth is more posterior than in *Armillifer armillatus* and *Porocephalus crotali*, although the relative positions of mouth and hook-pits vary a little; possibly this is due to the fact that the movement of the retractile hooks in some cases draws the hook-pits backwards and forwards. The terminal portion of each hook is rather short, but sharply curved.

The terminal segment is small, narrow, and very sharply pointed. The last two annular grooves are usually incomplete ventrally, and sometimes the terminal one is altogether obliterated. The anus is subterminal. The vaginal opening is larger, and is situated on a swelling about 2 mm. in front of the anus, between the terminal and penultimate segments.

Stigmata arranged in about five irregular rows.

*Male.* Length 20-35 mm.; width across cephalothorax 2 mm.; number of rings 27-30 (as in female).

In general appearance, shape, hooks, &c., the male resembles the female, but differs from it in size and in the possession of a pair of backwardly-pointing, finger-shaped processes on each segment. These processes are situated one on each side, on the ventrolateral aspect of the segment. They are most marked anteriorly, and gradually diminish in size towards the posterior end.

This species was first described by Diesing in 1835 (22). Various authors have confused *A. moniliformis* with *A. armillatus* Wyman, from which, however, it is easily distinguishable by the number of rings and sharp caudal extremity. As mentioned above, Looss (57) believed the species described as *A. moniliformis* and *A. armillatus* to be identical, and ascribed the discrepancy in the number of rings to the fact that rings which were indistinctly marked in the immature forms became clearly developed in the adult. This is certainly incorrect, and the two species are quite distinct. Usually, too, *A. moniliformis* occurs in the Oriental region, and Dr. Sambon has therefore concluded that it is most unlikely to occur also in the African. Nevertheless, one of the figures given by Looss of a Linguatulid from the West African Python (*P. sebae*) shows a typical specimen of *A. moniliformis*. There is also an example of *A. moniliformis* in the Oxford Museum from the same host. Further, I have



identified a larval form of this species from *Proteles cristatus*, a native of Africa. The specimen came from the Zoological Society's Gardens, and may therefore have been accidentally infected, but this is unlikely, and it looks as if *A. moniliformis*, or an allied form, occurs both in the Oriental and African regions.

*Additional hosts* :—

*Adult form* :—

(?) *Python sebae*, lung.

*Larval forms* :—

*Nycticebus tardigradus*, intestine.

*Felis viverrina*.

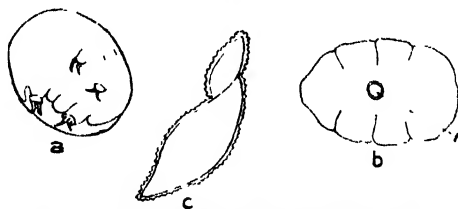
(?) *Proteles cristatus*.

#### Genus WADDYCEPHALUS Sambon.

##### WADDYCEPHALUS TERETIUSCULUS Baird.

This species shows considerable variation in size, number of annulations, etc. Baird's specimen, a female from the mouth of *Hoplocephalus superbis*, is 60 mm. long and has about 75 rings (2). According to Spencer (88) the length of the female is 12-32 mm., greatest width 5 mm., number of rings 65-70 (some of his specimens were, however, immature); length of male about 13 mm., width 2 mm., number of rings about 88.

Text-figure 12.



Embryo of *Waddycephalus teretiusculus* Baird.

- a. Ventro-lateral view.      b. Dorsal view; i, dorsal attachment.  
c. Outer integument.

I have examined a number of specimens from Australian snakes, and have come to the conclusion that Baird's specimen was an exceptionally large one. The majority of those I observed were from 20-30 mm. long, but in a few cases they reached 37-40 mm. The average width behind the head was 3-5 mm., but sometimes much less. Rings 50-70. The males were 6-7 mm. long, and one at least had only about 60 rings.

There is thus considerable variation both in size and in number

of rings. In the females this is especially noticeable. At first sight I imagined that the smaller and more slender female specimens were immature, as there is no doubt considerable growth after copulation, but on examination I found the uterus was long and coiled and some of the embryos were far advanced in development. The increasing size of the embryos may in some cases account for variation in girth, but not for the very great variation in length. Some of the male specimens may have been immature, but they measured less than 13 mm. (the figure given by Spencer), and in some cases the rings were only about 60.

On examining some embryos from the uterus of a female belonging to this species, I found that the outer envelope of some of the eggs was beset with small spiny projections. The envelope was detached by means of slight pressure on the cover-slip, when the embryo with two pairs of limbs and dorsal attachment was clearly visible, still enclosed by the inner integument. This spinous shell closely resembles that described by Noc and Giglioli (68) in their new genus *Samhonia*, and has not hitherto been observed in any other species of Linguatulid (text-fig. 12).

#### Section *LINGUATULINI* Sambon.

Dr. Sambon has created a new section: Linguatulini, with the following diagnosis:—"Body flattened and fluke-like, more or less convex in middle part of dorsal surface; sides depressed. Hooks disposed archwise. Alimentary canal axial. Uterovagina twines around it."

Thus the section Linguatulini differs from other Porocephalinæ mainly by the shape of body, which is flattened, with the middle part of the dorsal surface convex.

Leuckart (53) described the genus *Linguatula* as "possessing a body-cavity which forms a series of diverticula extending into the lateral portions of the annuli." This character certainly obtains in *Linguatula serrata* and also, I think, in Sir A. Shipley's specimen of *Subtriquetra*. In *L. serrata* the flattened portions contain a pocket-like diverticulum of the body-cavity in each annulus, the successive diverticula being separated by a series of dorsoventral muscle-fibres. There are also thickened bands of longitudinal muscle on the dorsal and ventral walls respectively. The axial rounded portion of the body contains the alimentary canal and reproductive organs. The lateral glands are entirely confined to the flattened lateral region, and occur between the dorsoventral bands of muscle. The presence of lateral diverticula is not, however, a matter of much specific importance; it is only a further development of the arrangement found in more cylindrical forms.

Dr. Sambon (78) has separated *Linguatula subtriquetra* from the other species of *Linguatula* (*L. serrata* and *L. recurvata*) and has created a new genus, *Subtriquetra*, to include the first-named

species together with *Porocephalus megacephalus* Baird. Of the four species above-mentioned, *Linguatula serrata* and *L. recurvata* differ from the others in the shape of the body, which is broad and flattened anteriorly and considerably narrowed towards the posterior end. In the new genus *Subtriquetra* the body is elliptical, and the greatest width is about the centre of the body. If this difference in shape is sufficient to justify the establishment of a new genus—and the difference is certainly very marked,—then it seems to me that Baird's specimen should be assigned to a separate genus, as it differs as much from *Subtriquetra* in this respect as it does from *Linguatula*. The head is very broad, and behind this it narrows rapidly, the posterior end of the body being almost cylindrical. The central portion of the body on the dorsal side is very convex, but the flattened lateral areas become gradually smaller, and finally disappear towards the posterior end of the body. In *Subtriquetra subtriquetra*, on the other hand, the whole body is elliptical, and the flattened area extends to the posterior end. In Shipley's specimen the dorsal area is very much more convex and conspicuous than in [*S.*] *megacephala*, while in *Linguatula serrata* it is not quite so marked. So that Baird's species really lies between *Linguatula* and *Subtriquetra* in this respect. Further, the hooks of [*S.*] *megacephala* are relatively much larger and more massive than those of *S. subtriquetra*. For these reasons I think that [*S.*] *megacephala* should be separated from the genus *Subtriquetra*, although both forms are parasitic in crocodiles. I have not suggested a new generic name because, as stated below, I believe that *Porocephalus kachugensis* Shipley may prove to be the immature form of [*S.*] *megacephalus*, and Dr. Sambon has already proposed a new genus, *Diesingia*, with *P. kachugensis* as type-species (78).

### Genus LINGUATULA Frölich.

#### LINGUATULA SERRATA Frölich.

This species was first described by Chabert (15*a*) in 1787, and since then a large number of observations have been made. The adult form occurs chiefly in the dog, wolf, and fox, the intermediate host being frequently a domestic animal—*e. g.*, sheep, ox, horse, goat, etc. Reference to the complete record of intermediate hosts will show, however, that the list is a long one, and it seems probable that the larval form can develop in almost any mammal, since experimental infection with various mammals has generally been successful.

I have in my possession specimens of ripe (?) *L. serrata*, sent me from the Veterinary College, Lahore, which measure only 35–42 mm. in length and 4–6 in breadth; so that either there is a considerable variation in size in this species, or else possibly my specimens belong to an allied species inhabiting the Oriental Region. I cannot, however, find any points of difference between

these Indian specimens and typical specimens of *L. serrata* except with regard to size.

*Additional host* :—

*Larval forms* :—

*Boselaphus tragocamelus* = *nilghai* (found by Dr. Woodland in India).

#### Genus SUBTRIQUETRA Sambon.

##### SUBTRIQUETRA SHIPLEYI, n. sp.

In 1910, Sir A. Shipley (85) described a Linguatulid from the pharynx of a crocodile which he assigned to the species *Linguatula* [*Subtriqueta*] *subtriqueta*. I have had an opportunity of examining this specimen in the Indian Museum, Calcutta, and add the following details:—It is a ripe female; length 20 mm., width 12 mm. The dorsal convex portion is extremely conspicuous. The rings are difficult to count, but there are about 30. The mouth is key-hole shaped, with the narrow end anterior. The hooks are simple and relatively small. A study of these details, together with the excellent figure given in Shipley's paper, make it clear that this parasite differs from *Subtriqueta subtriqueta* Diesing in shape, and probably also in convexity of the central part of the body. I think there is no doubt that it is a new species, for which I therefore propose the name *Subtriqueta shipleyi*.

#### LINGUATULINI INCERTÆ SEDIS.

##### PENTASTOMUM MEGACEPHALUM Baird.

The only known specimens of *P. megacephalum* were described by Baird (2) in 1853. They were three in number (apparently all female individuals), and had been found embedded in the flesh of the head of *Crocodilus palustris*. Some little time ago I was able to examine the specimens in the British Museum, S. Kensington. One was entire and measured about 20 mm. in length, the other two were broken—one was 20 mm., the other 25 mm. long. All three were about 10 mm. broad at the anterior end. As noted by Shipley (84) and Sambon (78), the body was so wrinkled that it was difficult to count the annulations, but these appeared to be about 50. The hooks were large and deep brown. Dr. Sambon mentions that these hooks had accessory spines, whereas Baird says that they were simple. I noticed a thickening at the proximal end of the hooks which I took to be merely the enlarged base, but I may have been mistaken. If the hooks are really double, this would be an additional argument for separating the species from the genus *Subtriqueta* (v. *supra*), where the hooks are single in the adult. The only entire specimen was a ripe female, the body of which was ruptured so that the uterus was

protruding. The larger of the two broken specimens was described by Baird as a male, apparently because (a) the uterus was not visible, (b) there was a small sharp papilla protruding from the posterior end which he imagined to be the penis. Since the males of all known Linguatulids are smaller than the females and the male genital aperture is always anterior, I think there is no doubt that this specimen is also a female, the posterior end being broken and a small portion of one of the internal organs—probably the alimentary canal—protruding. This specimen is not so wrinkled as the others, and the annulations are more clearly visible, especially on the ventral side, where there is a kind of groove separating the more flattened ventral portion from the lateral area, as shown in Baird's figure.

#### **POROCEPHALUS KACHUGENSIS Shipley.**

Body club-shaped. Length 9–12 mm.; width at anterior end 3.5–4 mm., at posterior end 1–1.7 mm. A pair of well-marked sensory papillæ present anteriorly. Mouth small, round, and slightly in advance of outer hooks; all markedly projecting and double. Rings difficult to count, but about 40, conspicuous on the ventral surface owing to the presence of fine chitinous rods at the margin of each annulus.

This species was first described by Shipley (85) in 1910 from parasites encysted in the liver of *Kachuga lineata*. I was allowed to examine these specimens and others obtained from the liver of *Batagur baska*, now in the Indian Museum, Calcutta, and published a further description of the species in 1921 (39). I then suggested that this might prove to be the larval form of *Porocephalus megagephalus*, and I still think this may be the case. As previously pointed out:—"In Baird's species the annulations were faintly marked on the dorsal surface, and the ventral surface was flattened and wrinkled. Length 20–25 mm., breadth of head 8–10 mm., body diminishing rapidly in size towards the tail. In *P. kachugensis* the length of the body is from 9–12 mm. and breadth of cephalothorax about 4 mm. These proportions resemble those of *P. megagephalus*, the difference in actual size being easily explained by difference in age." Further, some of the specimens show a definite insinking of the ventral face of the cephalothorax, and in older examples a small lateral flattened area is distinguishable on each side in the anterior half of the body.

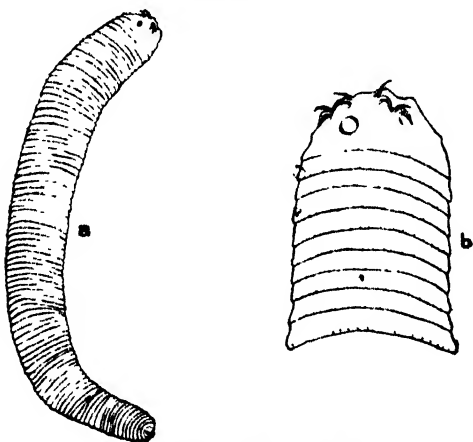
#### **POROCEPHALUS CROCODILI Wheeler. (Text-fig. 13.)**

Professor Wheeler (99 a) described a number of specimens of a Linguatulid found in the lungs and bronchi of *Crocodilus americanus*. Some of these specimens were encysted in the lung-tissue, some free in the bronchial cavity; they were mostly small and immature, but included an adult male and female sufficiently well preserved to allow of a clear diagnosis. According to the

author, one distinctive feature of these parasites was the presence of double hooks; and he therefore considered them to be related to *Raillietiella furcocerca* and *Pentastomum gracile*, where a similar structure was described by Diesing (22.23). The specimens described by Diesing were, however, immature; there is some uncertainty as to the adult form of *Pentastoma gracile*, but the mature *Raillietiella furcocerca* has single hooks. The presence of double hooks is frequently a sign of immaturity, and an immature specimen in its last stage may easily be mistaken for a young adult parasite, the double hooks being lost and replaced by single ones at the last ecdysis.

The description and measurements of Professor Wheeler's specimens show that, apart from the presence of geminate

Text-figure 13.



*Porocephalus crocodili* Wheeler.

a. Adult ♀, × 21. After Wheeler.

b. Anterior end of ♀, × 61. After Wheeler.

hooklets, the parasites resemble *Sebekia oxycephala* except in (1) number of annulations, (2) shape of cephalothorax. With regard to (1), the annulations in this genus are very numerous and difficult to count. Wheeler gives the number as 75 for one of his specimens, 105 for another. In *S. oxycephala* Leuckart (53) estimates the rings at "about 60." In the specimens I have seen they were 60 or more. This difference may therefore be set on one side. The probable identity of some specimens described as *Porocephalus crocodili* Wheeler and *Sebekia oxycephala* has already been pointed out by Dr. Sambon (78), who thinks it possible that Professor Wheeler described two species under one heading. If this is the case, it would help to explain the discrepancy in number of rings. (2) The shape of the cephalo-

thorax presents more difficulty. In *S. oxycephala* the anterior end is definitely narrowed and truncated. In figures of *P. crocodili* it is more or less rounded. The actual value of this distinction cannot be determined without seeing the specimens, but it may be pointed out that Wheeler's figures show a slight anterior narrowing, and there may be a certain amount of variation among individual specimens. Unless the character is very marked, this feature alone would not constitute a specific difference. The specimens resemble *S. oxycephala* in other respects—viz., length, shape of mouth, relative position of hooks, etc.; and, further, it is to be noted that they occur in the same host.

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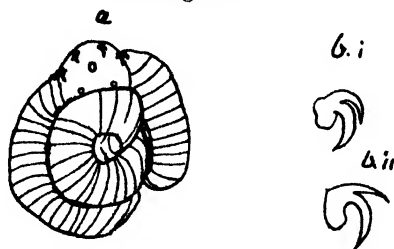
3. Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunningham, 1904-1905.—Report on the *Linguatulidæ*. By MARY L. HETT, B.Sc., F.Z.S.

[Received November 16, 1923 : Read February 5, 1924.]

(Text-figure 14.)

The *Linguatulidæ* collected by Dr. Cunningham in Lake Tanganyika were larval forms found encysted in the body-cavity and intestine of *Chrysichthys brachynema* Blgr. and of a "nunzi" (probably *Lates microlepis* Blgr.). Though immature, the specimens were well advanced in development. The body, which was coiled and twisted, was cylindrical and of about the same diameter throughout; when straightened, it measured about 24 mm. in length and about 1 mm. in breadth. The cephalothorax was rounded anteriorly, the posterior end slightly conical. The hooklets were double and projected well outwards. There was an oval armature round the mouth. The two anterior papillæ were small but well marked. The rings were numerous, about 100.

Text-figure 14.



? *Leiperia cincinnalis* Sambon. Larval form.

a. ♀, × 8.

b. Hooks—i., anterior; ii., posterior.

The resemblance of these parasites to *Leiperia cincinnalis* Sambon inclines me to think they may be young individuals of that species whose larval form is unknown, and this view is strengthened by the fact that Dr. Sambon has recently\* made the same suggestion with regard to two very similar immature specimens obtained from *Crocodilus niloticus*, the host of *Leiperia cincinnalis*. Like those mentioned by Dr. Sambon, these specimens from Lake Tanganyika resemble "*Pentastoma gracile*" Diesing, but the coiling of the Tanganyika specimens is remarkable, and unlike that of any other encysted *Linguatulid* that I have observed.

\* J. Trop. Med. London, xxv. p. 402 (1922).



4. On some Abnormal and Imperfectly Developed Specimens of the Sea Urchin *Echinus esculentus*. By H. C. CHADWICK, A I.S.\*

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(Text-figures 1-7.)

The specimens here described were collected at various points around the south end of the Isle of Man during the summer of 1922. Unfortunately, in every case the spines and viscera had been roughly removed by fishermen before the tests came into the writer's hands, so that no comparison of the radial water-vessels with the imperfectly developed ambulacra was possible. Though some zoologists may regard such specimens as mere curiosities, unworthy of more than passing notice, it seems desirable that their abnormalities and imperfections of development should be carefully examined, recorded, and illustrated. Many have already been described †; and, while there seems to be no limit to the possible combination of variants in an individual, the imperfections of development appear to follow certain lines and to indicate that a large proportion of them is due to arrested development and, possibly, displacement of one or more of the lobes of the hydrocoel of the larva. Specimens A and B, especially the latter, show that considerable modification of the normal shape of the test may occur without disturbance of its symmetry or imperfect development of its plates. On the other hand, more or less disturbance of symmetry always appears to be associated with imperfect development of the plates, especially those of the ambulacra.

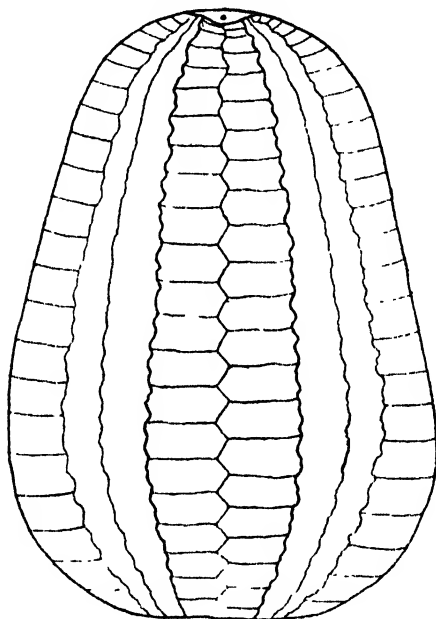
**Specimen A** (text-fig. 1) is remarkable on account of the exceptional disproportion between the height of the test and its diameter, the former being 8.8 cm. and the latter 6.3 cm. The five double columns of ambulacral and interambulacral plates are present, and, except for very slight elongation in the plane of amb. V and interamb. 2, the apical system is normal in shape and number of plates. At the apical pole the five ambulacra, especially those of the trivium, are distinctly convex—almost protuberant, and even at the ambitus give to the test, when viewed from the apical pole, the form of a pentagon with rounded angles. The ambulacra vary considerably in depth, but all consist of the normal number of three elements, each with its

\* Communicated by F. A. BATHER, F.R.S., F.Z.S.

† See full bibliography by R. Koehler, 1922 : "Anomalies et irrégularités du test des Échinides." Bull. Inst. Oceanogr. Monaco, No. 419.

pore-pair. They show a marked tendency to overlap the adjacent interambulacra along the sutural line, which consequently is more than usually irregular and obvious. The interambulacra show a disproportion of depth to width corresponding to that of

Text-figure 1.



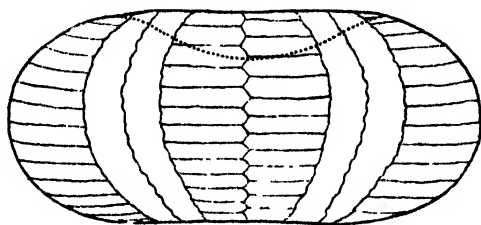
Abnormal elongation of vertical axis.

height to diameter of the entire test. There are 26 to 28 plates in each column. In spite of exceptional disproportion this specimen does not present any deficiencies such as partial or entire absence of ambulacra or interambulacra.

**Specimen B** (text-fig. 2) also is remarkable for the exceptional disproportion of its principal dimensions. The height of the test, measured from the apical system to the peristome, is 2.5 cm., and its diameter at the ambitus 6.7 cm. The apical system, however, lies at the bottom and in the centre of an almost completely symmetrical depression of the apical area of the test. This depression, measured through the madreporic plane, is 4 cm. in diameter, and, in interradius 4, is slightly deeper than elsewhere. Measured from the margin of the depression to the oral face, the height of the test is 3 cm. The normal number of five double columns of ambulacral and interambulacral plates

occurs, and all the plates are normal in size, composition, and arrangement.

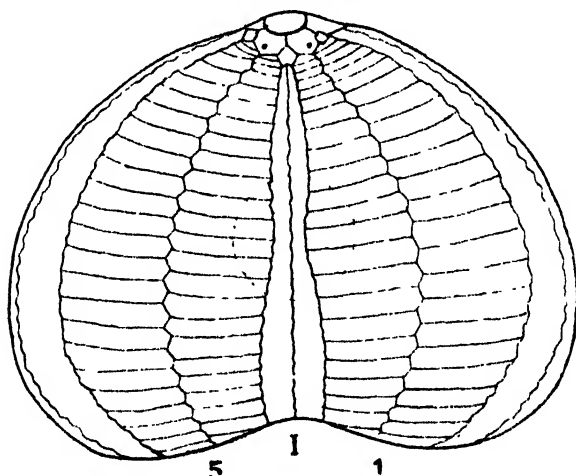
Text-figure 2.



Depression of apical pole.

**Specimen C** (text-fig. 3) is of average size and proportions, its height being 6.2 cm. and its diameter at the ambitus 8.2 cm. The symmetry of the test is disturbed by a lateral flattening of which radius I is the median line, and about midway between the oral and apical ends of amb. I there is a well-marked depression. The width at the ambitus of amb. II to V is 1.8 cm. each, and,

Text-figure 3.



Imperforate ambulacrum.

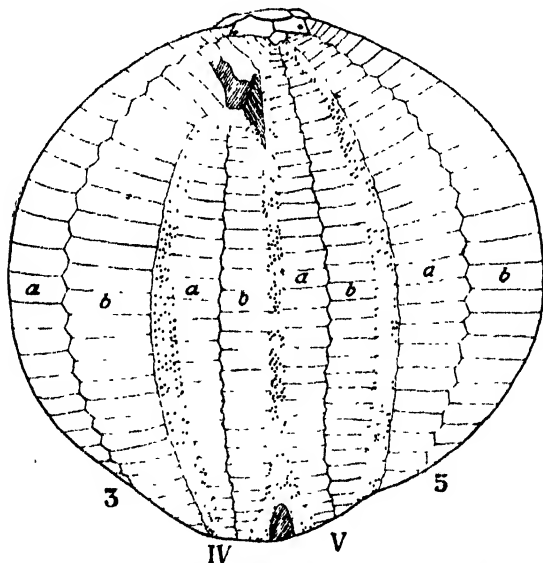
except for very slight curvature of II, III, and V, they are normal. The apical system is normal, except for slight elongation in the plane of radius I and interradius 3. The width at the ambitus of amb. I is 7 mm., so that it is less than half the width of its fellows. At the point where the above-mentioned depression is most marked the gradual narrowing of the



ambulacrum, as it approaches the apical pole, is disturbed by slight contraction. Sutural lines show that the plates of this ambulacrum are of normal composition. Ocular plate I bears the usual pore, but this is smaller than those of its fellows. The two last-formed plates of amb. I are of nearly equal size and each has a single pore. The next plate in column *a*, that in contact with interamb. 5, is of much larger size, nearly quadrangular, and has a single pore. The next plate is much deeper than wide, and, though it shows sutural lines and two minute pits or punctæ close to the border of its single tubercle, it is imperforate. The next plate also is imperforate. The next two plates consist each of two components of nearly equal size and shape. One of each of these is punctate, but both are imperforate. Plate 12 in this row has an isolated component which is punctate, but beyond this point all the plates of the column are imperforate. The second and third plates in column *b* bear each a minute puncta. All the remaining plates of this row are imperforate.

**Specimen D** (text-fig. 4).—Irregularity of the apical system, truncation of amb. IV, and almost complete suppression of interamb. 4 constitute the remarkable features of this specimen.

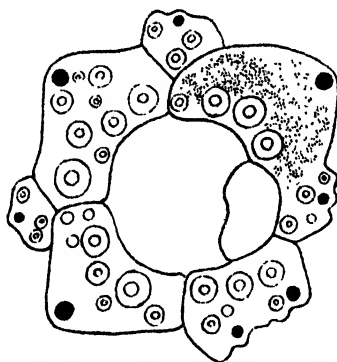
Text-figure 4.



Almost complete suppression of interambulacrum 4.

The height of the test is 7 cm., and its diameter at the ambitus 7.7 cm. These dimensions show that the specimen is more globose

than the great majority of those found in Manx waters. Amb. I, II, and III are normal in composition and nearly so in relative position, though when the test is oriented according to Loven's formula the left border of No. 1 is exactly posterior. Interamb. 1, 2, and 5 are normal, except that, in consonance with the irregularity of the apical system, the apical ends 2 and 5 are wider than those of their fellows. At its apical end amb. IV is cut off from the apical system, and the intervening space is partly filled by lateral extension of the plates of interamb. 3. For rather more than two-thirds of its length the right border of amb. IV (column *b*) is in contact with the left border of amb. V (column *a*). In both these columns the plates appear to be compressed in the direction of their length. As a result of this the width of the perforated portions combined is less than that of one column of one of the normal ambulacra, and it is scarcely possible to trace the line of suture. The plates of column *a* of

Text-figure 4 *a*.

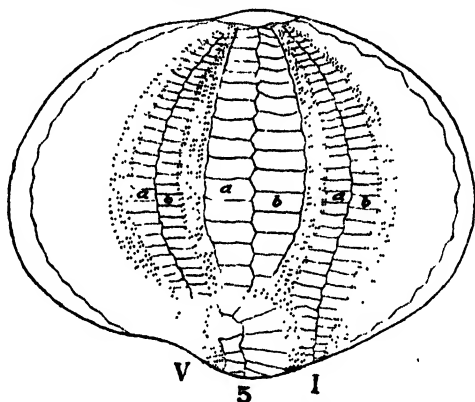
Irregular composition of apical system.

amb. IV are considerably wider than those of column *b*, and do not appear to have been affected by lateral compression. The oral ends of these two closely approximated ambulacra are separated by a small islet, 4 mm. long, of the almost completely suppressed interamb. 4, and at the apical end the same interamb. is represented by four or five plates of irregular shape. In text-fig. 4 the plates of interamb. 4 are indicated by shading. The apical system consists of seven plates (text-fig. 4 *a*). Four of these are genitals, corresponding in position to interamb. 1, 2, 3, and 5. But two of these plates, viz. 1 and 2, function also as oculars, inasmuch as they have two perforations, the supernumerary one being in each case opposite the apex of an ambulacrum, where the ocular is absent. Normal oculars occupy their usual positions at the apical ends of amb. III and V. Wedged in between genitals 1 and 2, and on their *inner* edge bordering the periproct, is a

seventh and evidently displaced plate. It is imperforate, but its shape is roughly that of an ocular, and it appears to be ocular II.

**Specimen E** (text-fig. 5).—The general shape of the test, when viewed from the apical pole, is that of a well-rounded oval, due to incomplete development of interamb. 5. The height of the test is 4.8 cm., and its longer diameter at the ambitus 5.7 cm. At their adoral ends amb. I and V approach each other so closely as to isolate the adoral end of interamb. 5. Compared with its fellows 2 and 3 on the opposite side of the test, the latter is greatly reduced. In both columns the plates are clearly recognizable as far as the sixteenth, counting from the apical pole. Beyond this point, at which amb. I and V approach each other most closely, there appear to be nine or ten plates in each column; but their shape is so much modified by lateral pressure

Text-figure 5.



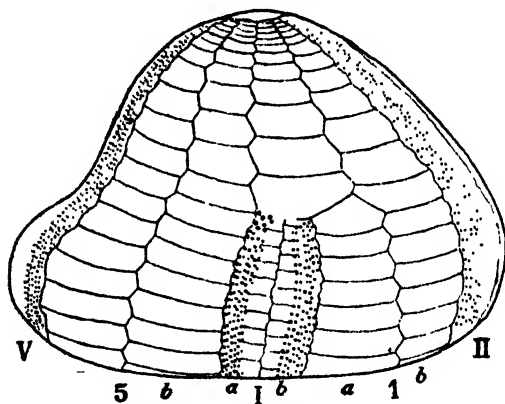
Incomplete development of interambulacrum 5.

that it is scarcely possible to speak with certainty. Plate 16 of column *a* carries six ambulacral pores (probably three pairs), and in column *b* continuity is interrupted by the intrusion, between plates 19 and 20, of the porous portions of two or three plates of column *a* of amb. I. No actual breach of continuity of the plates of column *b* of amb. I occurs: in column *a* there is slight dislocation and almost complete obliteration of a few pore-pairs close to the point of intrusion just named. At the adoral end of amb. V and at the margin of the peristome there are five almost normal plates of column *b*. The next two plates are reduced and deformed by lateral pressure and intrusion of several plates of column *a* of interamb. 5. In like manner a few, perhaps four, plates of column *a* of the same ambulacrum are isolated. There is, indeed, at this point a narrow isthmus of interambulacral

plates connecting interamb. 4 and 5. Beyond it are three or four much compressed plates of column *a*, and these are succeeded by a long series of normal plates as far as the apical system.

**Specimen F** (text-fig. 6).—The height of the test is 5.3 cm., and its diameter at the ambitus 6.9 cm. The apical system is symmetrical in shape and consists of the normal number of plates. The interest of the specimen lies in the abrupt truncation of amb. I and IV, and the contraction of amb. II, III, and V at about the same level of the test in each case. All the plates of amb. I are perfect in composition, though reduced in width up to a point a little above the ambitus. The ambulacrum as a whole trends forward and to the right instead of taking a straight course to oc. I; and the suture which separates the plates of column *a* of interamb. 1 from those of column *b* of interamb. 5 is continuous with that which separates the latter from column *a* of amb. I. Counting from the apical system to truncated amb. I,

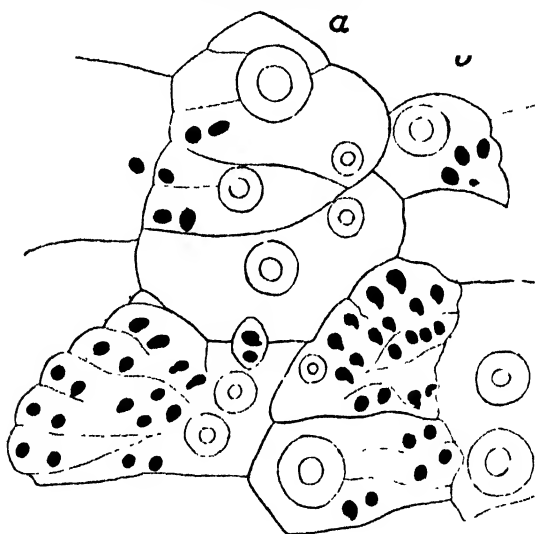
Text-figure 6.



Truncation of ambulacrum I.

there are in column *a* of interamb. 1 eleven plates. The eleventh plate is not only in contact with the last-formed plates of amb. I, but is not clearly marked off by suture from that in column *a*. The latter and the next plate in the same column have each two pore-pairs. The last-formed plate in column *b* is of irregular shape, but has three pore-pairs. The truncation of amb. IV occurs at almost the same level as that of amb. I. Like the latter it trends forward and to the right, and the suture which separates it from column *b* of interamb. 3 is continuous with that which separates the latter from column *a* of interamb. 4. The last-formed plate of column *a* of amb. IV is roughly pentagonal (text-fig. 6*a*). It consists of an adoral primary plate with a pore-pair and two demi-plates which are imperforate. The next is a larger plate of the

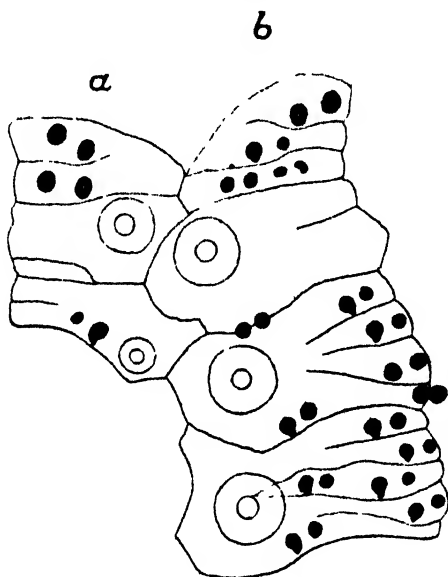
same composition. The pore-pair of the smaller, aborally-placed demi-plate trenches upon the adjoining interambulacral plate; indeed, the outer pore is in the latter. At first sight the adorally-placed primary appears to be imperforate, but it is possible that its pore-pair may be found in a very small included plate wedged in, almost at right angles to the normal position, between the primary and the next plate. Owing to displacement of the pore-pairs and partial obliteration of the sutures, the composition of the next (?) three plates is not easily determined. In like manner the composition of the (?) four last-formed plates of column *b* is obscured, and these, like the imperfectly formed plates of column *a*, are preceded by a series of perfectly formed plates.

Text-figure 6 *a*.

Irregular composition of plates of truncated ambulacrum IV.

The actually last-formed plate in column *b* is isolated by the intrusion between it and its predecessors of an adjacent interambulacral plate. Amb. II, III, and V are composed of perfectly formed plates, except at the points where they are slightly constricted. Here, in column *a* of amb. II (text-fig. 6 *b*), there is a plate, much deeper than its neighbours and composed of three elements, the adoral of which is imperforate. Next to it, adorally, is a small plate, the adoral element of which only has a pore-pair. In column *b*, at about the same level, there is a plate composed of three elements, the adoral primary of which has two pore-pairs. Next to it, adorally, there is an imperforate plate, unless a very small pore-pair actually in the line of suture

between it and the next plate belongs to it. The next plate consists of four elements, the adoral of which has two pore-pairs; and the next of five elements, the middle one of which, a demi-plate, also has two pore-pairs. In amb. III the constriction is very slight. Here, in column *a*, there is a plate consisting of an adoral primary and two demi-plates, the aboral of which is imperforate. This is succeeded by a rather large subtriangular demi-plate and this again by two ill-defined plates containing

Text-figure 6 *b*.

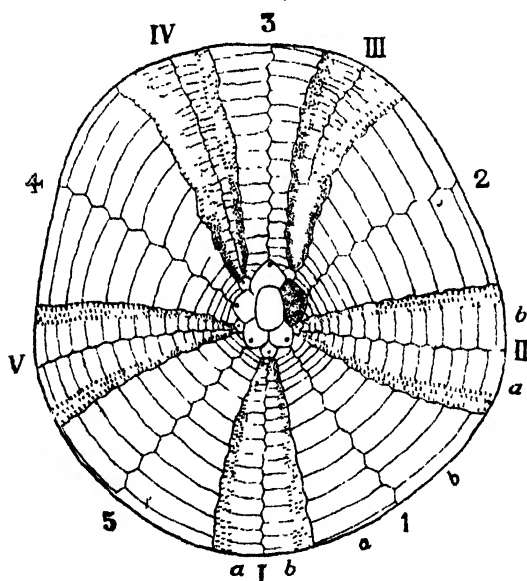
Irregular composition of plates of truncated ambulacrum II.

between them seven pore-pairs. In column *b* the plate corresponding in position to the first-named in column *a* is of the same composition. The aboral demi-plate is imperforate, but the adoral primary has two pore-pairs. In column *a* of amb. V there are imperfectly defined plates containing between them eight pore-pairs and an odd pore. At the same level in column *b* there are three imperfectly defined plates containing between them eleven pore-pairs. Plate 12 of column *b* in interamb. 2 has a single pore-pair well within its borders.

**Specimen G** (text-fig. 7).—The imperfection in development of this specimen is associated with considerable depression of that portion of the test which is traversed by amb. III and IV. The height of the test is 5.5 cm., and its diameter 7.2 cm. The

height is slightly reduced by the fact that the apical system is involved in the depression of the test. It is also slightly elongated in an antero-posterior direction, and its anterior border is depressed. The depression of the test is rather greater over amb. III than over amb. IV; but the result is practically the same in both cases. It is not possible to give a detailed description of the plates of these ambulacra. For nearly 1.5 cm. from their apical ends the inner, imperforate portions of their plates are much reduced in width, and the perforate portions of the more apical ones present a distinct appearance of imbrication

Text-figure 7.



Depression of anterior portion of test.

as a result of lateral pressure. At about 2 cm. from their apical ends the two ambulacra begin to widen out until, at their oral ends, they are as wide as the normal ones. At a point a little nearer the peristome the plates, especially those of column *a* in amb. III and of column *b* in amb. IV, gradually assume the normal composition and character. Interamb. 3 is correspondingly affected by the depression of the test. Its plates are much reduced in width throughout its length, especially those of column *a*.

5. On a new Giant Salamander, living in the Society's Gardens. By E. G. BOULENGER, F.Z.S., Director of the Aquarium.

[Received January 2, 1924: Read March 4, 1924.]

The Zoological Society early last year received a notification from the Marquess of Sligo, who was then in Peking, that whilst recently visiting Hong Kong he had come across a giant salamander which was living in captivity in the Botanical Gardens there, and that he had prevailed upon Sir Reginald Stubbs, the Governor of the Island, to present it to the Society. Although a giant Chinese Salamander had been described by Blanchard\* under the name of *Sieboldia davidiana*, by most authorities the giant salamander of China was regarded as identical with *Megalobatrachus maximus* of Japan. I have myself examined a number of Chinese specimens in the British Museum collection, and can find no distinction between them and the previously described Japanese species. We naturally assumed that the Hong Kong specimen would prove to be the well-known and only Old World species which occurs in the mountain streams of both Japan and China. On arrival in our gardens early in June, the salamander, a large specimen measuring 99 cm. in length, appeared to me to differ in various respects from any salamander previously recorded. Investigation showed that not only was the head longer and flatter than in *Megalobatrachus maximus*, and without the characteristic tubercles of that species, but that the nostrils were much more widely separated from one another. As a result of there being no prominent tubercles on the head, the eyes, which in *M. maximus* are scarcely discernible with the naked eye, are in this Hong Kong specimen quite prominent. I have therefore no hesitation in describing this salamander as new, and I name it *Megalobatrachus sligoi*, after the Marquess of Sligo, who was responsible for securing the animal for the Zoological Society.

*MEGALOBATRACHUS SLIGOI*, sp. n.

Habit stout. Head large, very much depressed; snout rounded; nostrils small, widely separated; eyes small but prominent; the distance between the eye and the labial border contained three and a half times in the distance between the nostrils. Body squat, depressed. Limbs short, stout; fingers and toes depressed; outer fingers, toes, and fibula bordered with membranes. Tail short, strongly compressed, finned, and the end

\* Compt. Rend. Acad. Paris, lxxii. 1871.



rounded. Skin with a few minute tubercles on the body, none on the head; a thick cutaneous fold along each side. Coloration:—Brown spotted with black.

From *Megalobatrachus maximus* it differs, among others, in the following important points:—

*M. maximus.*

Head flattish, covered all over with prominent tubercles; one seventh total length.

Distance between eye and labial border contained  $1\frac{1}{2}$  times in distance between nostrils.

*M. sligoi.*

Head very flat, smooth; one-fifth total length.

Distance between eye and labial border contained  $3\frac{1}{2}$  times in distance between nostrils.

The Marquess of Sligo has kindly provided me with the following notes on the history of this interesting batrachian:—

“In April 1920 there was an unusually violent storm of wind and rain in Hong Kong which did much damage to the Botanical Gardens. Among other damage, it caused an 18-inch drain to be choked, causing in its turn the pipe to burst. The result was the scouring out of a long length of drain and much ground round about it. The giant salamander was found on the scour, having evidently been washed down from somewhere, and thrown out at the end. Since its capture it lived in a circular basin 4 feet in diameter with 6 inches depth of water. It was fed once a day on live tadpoles. At times when the supply of tadpoles ran short, small quantities of raw beef were substituted.”

Sir Reginald Stubbs informs me that it is practically certain that the new salamander is not a Hong-Kong-born creature. It appears that specimens which have from time to time been brought over from the mainland and been placed in the fountain in the Botanical Gardens have escaped. It is therefore highly probable that the salamander under discussion is one of these animals.

6. Reversible Evolution, with Examples from Fishes. By  
C. TATE REGAN, M.A., F.R.S., F.Z.S., Keeper of  
Zoology in the British Museum (Natural History).

[Received November 26, 1923: Read February 5, 1924.]

Of all the so-called "laws" of evolution that have been formulated, that of the "irreversibility of evolution" has perhaps a more general application than any. Such a law as that which states that evolution involves a decrease in the number of elements of a metameric series has but little value, for there is plenty of evidence that their number may be increased; but there are not many exceptions to the law of irreversibility, which states that an organ, once lost, cannot be redeveloped in its original form and that an organ, once changed, cannot revert to its original structure. After hearing Baron Nopcsa's remarks on this subject at a meeting of the Zoological Society on November 20th, 1923, it seemed to me worth while to put on record some exceptions to the law of irreversibility which appear to be less open to criticism than most of the examples that he gave.

The Loricariidæ (cf. Regan, Tr. Z. S. 1904) are a family of Siluroid Fishes found in the rivers of South America, and are characterized by having the body protected by series of bony plates. If the evolutionary history of these bony plates be considered we find that in the Selachians the body is covered with denticles which are structurally similar to teeth, that in the earliest bony fishes there are juxtaposed rhombic bony plates, or "ganoid scales," on the surface of which the denticles may persist, and that in the earliest fishes with a truly homocercal caudal fin the scales are cycloid, that is, thin, rounded, and overlapping, without denticles; such cycloid scales are found in the more primitive Ostariophysi (Characinidæ, Cyprinidæ), but the more specialized Ostariophysi, the Siluroids, have lost them and are naked, unless they have secondarily acquired a covering of bony plates.

The bony plates of the Loricariidæ differ in histological structure from ganoid scales, but on their surface they bear conical denticles which are formed of dentine and enamel. Here we appear to have a genuine example of the redevelopment of an organ that has been lost, although, perhaps, the fact that the Loricariidæ have teeth in the jaws makes the development of structures homologous with teeth on the bony plates covering the body somewhat less marvellous. However, it seemed to me so curious that the skin of fishes, whose more remote ancestors had cycloid scales and whose more immediate ancestors were naked, should have retained, or regained, the power of forming denticles of

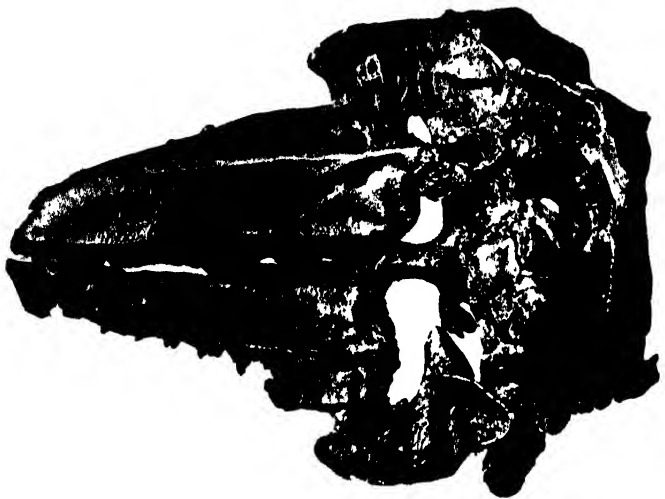
the Selachian type over the whole surface of the body, that I gave Mr. C. T. Carter some material and suggested that he should examine it; the result is that he has described these denticles as formed of true dentine, capped with enamel (P. Z. S. 1919, ii. p. 321).

The mountain streams of the Andes are inhabited by some dwarfed Loricariids (*Arges*, or *Cyclopium*) that have lost their armour, and are naked,—in this reverting to the primitive Siluroid condition. In the armoured Loricariidæ the adipose fin is a triangular flap of skin, the anterior edge of which is supported by a strong movable spine; in some of the naked mountain forms it has the same structure, but in others the fin is more fleshy and the spine is reduced, and in others again the spine has disappeared and the adipose fin has reacquired the typical Siluroid structure; these differences are shown in the figures illustrating my monograph (Tr. Z. S. xvii. 1904, pl. xxi). Here we have clear evidence that an organ has changed, and has afterwards reverted to its original structure.





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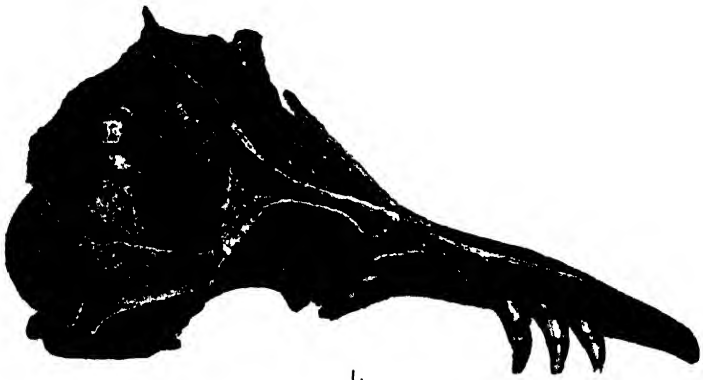


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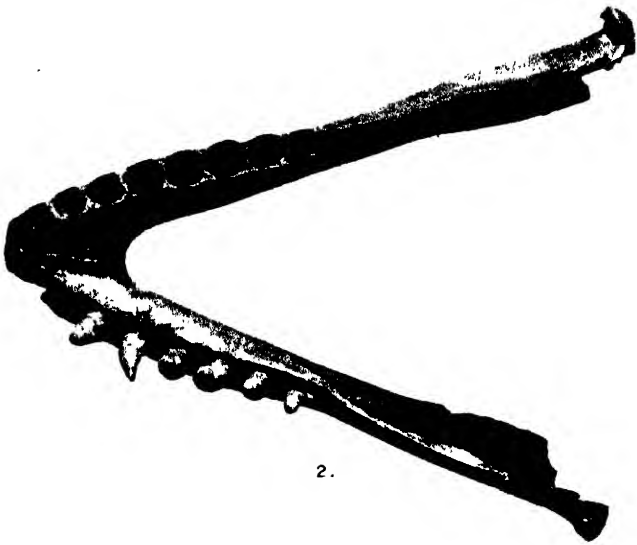
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PSEUDORCA CRASSIDENS.





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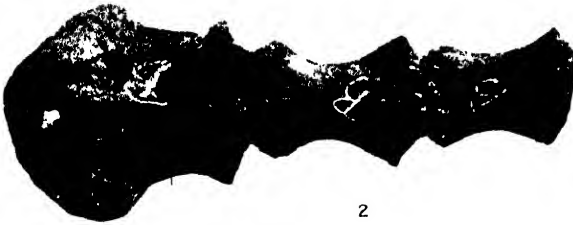
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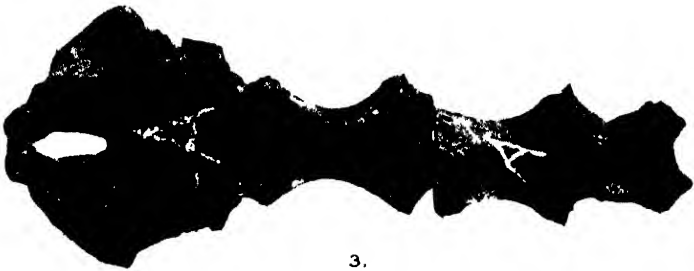




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PSEUDORCA CRASSIDENS.

# 7. Two Skeletons of the Cetacean *Pseudorca crassidens* from Thorney Fen. By J. R. GARROOD, M.D.\*

[Received October 13, 1923 : Read November 20, 1923.]

(Plates I.-III.†; Text-figure 1.)

These two skeletons were found in a similar situation to that of the type-specimen of this genus, which was first described by Sir Richard Owen (1846) in 'British Fossil Mammals and Birds,' p. 516. He says:—"In 1843 there was discovered in the Great Fen of Lincolnshire, beneath the turf, in the neighbourhood of the ancient town of Stamford, the most complete example of the skeleton of a cetaceous animal, which is now preserved in the museum of the Stamford Institution. The skull is almost entire, and some of the teeth are preserved in the lower jaw."

Sir William Flower (1884) states "This skull is lost," and in his copy, now in the British Museum (Natural History), of Gray's Catalogue of Seals and Whales (1866, p. 290), there is a manuscript note by him, referring to the type-specimen of *Pseudorca crassidens*:—"lent to Prof. Owen and never returned. Secretary Stamford Institute, 1866."

I have made inquiries at Stamford, and apparently the skull was not there when some of the contents of the museum were sold, neither is it at Lincoln nor at Spalding, to which places parts of the collection were taken.

Sir Richard named the animal *Phocæna crassidens*, and compared the skull with those of *Phocæna orca*, *P. melas*, and *P. leucas*. He regarded it as an extinct species "until it should be proved that it still existed in our seas."

This proof was not very long in coming, for on November 24th, 1861, more than a hundred of these animals arrived at dawn in the bay of Kiel, having strayed, like their ancestors, into narrow waters. About thirty were separated and one of these was killed in the harbour. It was a female sixteen feet long, was exhibited in Holstein, and finally bought for the University of Kiel.

A plaster model was made and a photograph taken. This last forms the basis of the woodcut which heads Sir William Flower's English edition of Reinhardt's Monograph (1866).

Japha (1908, pp. 154-171) states that of this group the Malmö and Båstad specimens are in the museum of Lund, and that the Ystad specimen is at Upsala. He also gives a good account of the finding and disposal of this Baltic school.

\* Communicated by Sir S. F. HARMER, K.B.E., Sc.D., F.R.S., Vice-Pres. Z.S.

† For explanation of the Plates see page 193.

In the summer of 1862 three dead specimens were thrown up on the shores of the islands of Zealand and Funen. These were the Refsnaes, Asnaes, and Middelfart specimens, which form the material of Reinhardt's Monograph (1862-1866). They are preserved at Copenhagen.

Another specimen, cast up on the coast of Holland in the same year, is at Göteborg.

In 1864, Mr. W. L. Crowther, of Hobart Town, sent two skulls to the museum of the Royal College of Surgeons under the name of "Blackfish." They were described by Sir William Flower (1864, p. 420) as *Orca meridionalis*, but afterwards he stated that no specific difference existed between them and *Pseudorca crassidens*. Later, other specimens were sent from Adventure Bay, Tasmania. Two are in the museum of the Royal College of Surgeons; one is in the British Museum (Natural History), 1506 a, see Flower's 'List of Cetacea, British Museum,' 1885; and a skeleton and a skull are in the Zoological Museum at Cambridge University. These two were presented in 1866. In addition, there are in the British Museum a skeleton (5.7.23.1, Travancore), presented by the Director of the Trivandrum Museum, and a lower jaw (47.6.2.1 = 361 a, no locality).

Cope (1866, p. 293) described a beak and mandible from off Paita, Peru, under the name of *Orca destructor*, but True (1889, p. 145) regarded the specimen as identical with *P. crassidens*.

A specimen found on the coast of the Argentine in 1868 was sent to the museum of Buenos Ayres, and described by Burmeister (1879, p. 538) as *Globicephalus grayi* and later as *Pseudorca grayi*; he compares it with *Globicephalus srineval* of Europe, and states that he saw several of these swimming in the sea. An illustration of these makes them appear like *Globicephalus melas*, but True (1889, p. 145) has no doubt that the skull is identical with that of *P. crassidens*.

True (1889, p. 144) has reported upon a skull in the U.S. National Museum which was stated to have come from the north-east coast, probably Davis Strait, but Miller (1921, p. 205) thinks this is doubtful. There are also a mandible and beak with teeth in this museum.

In 1903, Ferguson described a specimen from Travancore. His figure is reproduced in the British Museum Guide to Whales, Porpoises, and Dolphins, 1909, 1922.

Miller (1921, p. 205) described a much weathered skull and imperfect skeleton from one of the Aves Islands in the Caribbean Sea, 70 miles from the coast of Venezuela. It was received in 1883. Similar specimens were brought from Pichilingue Bay, Lower California, in 1888.

A skeleton, nearly complete, was found near Princetown, Florida, and it appears probable that four individuals were stranded there. Miller also describes another specimen entered as having "No History."

W. R. B. Oliver (1922, p. 577) states that in March 1906 a

school of several hundreds were stranded on Long Beach, Petre Bay, Chatham Island. These were identified by him, when he saw many of the remains in December 1909, as *Pseudorca crassidens*. Teeth in upper jaw, eight in each side. There is also a cranium in Dominion Museum, Wellington, from Lyall Bay.

Lastly, we come to the two specimens which are about to be described, and which were dug up towards the end of 1921.

Thus we see the number of specimens of which we have remains in museums is less than thirty altogether.

A general account of *Pseudorca crassidens* is given by Flower (1883, p. 507), in which he states that he is unable to detect any constant differences in perfectly adult specimens of the Danish and Tasmanian groups.

Another general account is given by True (1889, p. 186), and he gives the synonymy on p. 143, coming to the same conclusion as Prof. Flower.

On October 15th, 1921, a tooth was brought to me by Mr. Aubrey, of Weybridge, Alconbury, on whose farm at Thorney, together with a quantity of bones, it had been found. These had been found while earthing up the crop of celery.

I identified the tooth, after having seen some of the vertebræ, as that of a whale, and Mr. C. Forster-Cooper suggested the possibility of the specimens being *Pseudorca crassidens*, which indeed they proved to be.

The site of the discovery was on Bassenhally Moor, a part of the Cambridgeshire fens between Whittlesea and Thorney, a short distance from the river Nene, which is artificially banked up, the ground being at or near sea-level. This is not the old course of the river, and the banking was first done by Morton, Bishop of Ely, in the 15th century. The cut is known as Morton's Leam, but there is evidence that some banking of the fens was done during the Roman occupation, and the "Fen Road" lies a little to the south of the site.

The soil consists of a black earth about 9 inches thick, overlying a yellow clay. As a result of cultivation and the removal of crops, the earth is rapidly getting shallower. Prof. Marr has examined specimens of the soil, and considers that the vegetable matter is recent and the clay a comparatively modern alluvial deposit.

The bones on being treated with a mineral acid leave no formed residue, but they do not appear to be mineralized. A piece of human bone which had been buried four or five hundred years kept its shape, though completely decalcified by acid, and the same is true of a specimen from a round barrow in Somerset.

It is stated that a boat was dug up in a neighbouring field some years ago, and a skeleton of *Orcinus orca* was found in Whittlesea Mere when it was being drained. This is in the Peterborough Museum.

These fens are continuous with those near Stamford, so that it is not impossible that my two specimens belonged to the same school as the specimen described by Sir Richard Owen, and the circumstances of their stranding in the head-waters of the Wash may not have been unlike those of the Kiel Bay school, which lost itself in the narrow sounds of Denmark.

The two skeletons lay alongside each other with spines crossing in the caudal region, their heads pointing inland to the East and lying fully extended. The bones were not much disturbed, but one pectoral fin was washed back to the region of the tails. Some time after I got these skeletons, I ascertained that Mr. Phillips, of Peterborough, had a mandible which, when placed in position, fitted one of my skulls. Apparently it was brought to him before the other parts of the skeletons were discovered. He has very kindly given it to me.

The bones were of a light cream-colour except where stained by clay. They lay at the junction of the black earth and yellow clay already mentioned. I have treated them with shellac as they were rather friable.

Many of the bones, and particularly those of the head, are much damaged. The latter were first found, and were much broken by labourers' tools and unskilful handling. Those which were got out by Mr. Forster-Cooper, Mr. Aubrey, and myself were less damaged. The first lot of bones made several journeys in a sack before they came into my possession!

I shall refer to the specimens as A and B, A being slightly larger than B. They are approximately 14 feet long, which is substantially that of other adult specimens. The other measurements correspond generally.

#### *Age of the Specimens.*

Sir William Flower (1864, p. 469) has shown that this may be determined by the condition of the osseous tissues. In the light of his account, I conclude that these two animals were nearly full-grown, for

1. The spinous processes of the vertebræ are fairly rounded.
2. A number of the vertebral epiphyses are ossified to the centra, viz.

In A the 1st cervical to the anterior epiphyses of 2nd dorsal inclusive, and the 12th caudal to the end.

In B the 1st cervical to the 6th dorsal inclusive, and the 7th caudal to the end.

3. The epiphyses of the humerus and the upper epiphysis of the radius are ossified to the shafts.
4. The basisphenoid, presphenoid, and basioccipital are united, as is the exoccipital to the supraoccipital.

These facts indicate that the animals were not young ones.

They were not very old, for

1. The epiphyses of the central portions of the spine are separate from the bodies of the vertebræ.
2. The lower epiphyses of the radius and ulna are not completely united to the shafts.
3. The sterna have not all their segments united by bone.

Lastly, since size is perhaps the most reliable factor in the determination of age, their length of about 14 feet corresponds with other known adult specimens of *Pseudorca crassidens*.

I think, therefore, that my specimens A and B are young adults, and that specimen B is older than A, for

It has more vertebral epiphyses ossified.

The suture between the supraoccipital and parietal has closed, whereas it is distinct in A. Though the suture between the supraoccipital and frontal is visible in B, it is much more firmly united than in A, in which, in fact, it was completely detached when I received the bones.

The mandible of A is not ossified at the symphysis, whereas that of B is firmly united.

Although the mandible of A is smaller than that of B, I think that there is no doubt that it fits the skull A, though this is larger. There is a similar disparity in the size of the upper jaws, which is a further indication that B is older than A, for all the jaw apparatus continues to increase with age.

It would appear hazardous to attempt to determine the sex in the absence of pelvic bones, which Eschricht (1866, p. 176) has shown in the case of the Northern species of *Orca* may be used for this purpose.

However, the following points may give a slight indication thereof.

Though the skull of A is slightly larger than that of B, the ridges for the attachment of muscles are not so well marked. This might be accounted for by the fact that it is younger, or a female, or perhaps both, for females are often bigger than males of the same age, and A is certainly younger than B.

Sir William Flower (1883, p. 470), quoting Fischer 1881, states that the mandible of the male of *Delphinus delphis* is longer than that of the female, and the rostrum of the male longer and narrower, while in *Delphinus tursio* the breadth of the skull is greater in the female where the height is the same, and the rostrum is broader at base and middle part.

My specimens agree with this, but the beak of B is broader than that of A.

Such evidence as there is points, I think, to A being female and B male.

#### *Skulls.*

Of the two, that of A is in rather the better condition. The placing of the broken fragments in position has been somewhat

difficult, but I have been helped by the fact that there are two skulls, and by the loan of one of the Tasmanian skulls from Cambridge by Mr. Forster-Cooper.

The following table of measurements (in inches) shows the relationship between A and B and Sir Richard Owen's Stamford skull, the Tasmanian skull above referred to, and the Refsnaes specimen of Reinhardt (1866):—

	Cambridge.	B.	A.	Reinhardt.	Owen.
1. Length of skull, back of condyles to end of beak...	22 $\frac{3}{4}$	24	24 $\frac{1}{2}$	24.7	26
2. Length of beak from notch	10 $\frac{1}{2}$	11 $\frac{3}{4}$	11 $\frac{3}{4}$	11.3	12
3. Breadth of skull across postorbital processes of frontals .....	13 $\frac{1}{4}$	14 $\frac{3}{4}$	14 $\frac{1}{2}$	14.7	15
4. Breadth of skull across zygomatic processes of temporals .....	13 $\frac{1}{2}$	14 $\frac{1}{2}$	15	15.3	15 $\frac{1}{2}$ ?
5. Height of skull from lower part of condyles to occipital crest .....	9	9 $\frac{3}{4}$	9 $\frac{3}{4}$	—	9 $\frac{1}{2}$
6. Breadth of beak at origin ..	7 $\frac{1}{4}$	8 $\frac{1}{4}$	8 $\frac{1}{4}$	8.5	—
7. Breadth of beak at middle part just anterior to posterior tooth but two .....	6 $\frac{7}{8}$	7 $\frac{1}{8}$	6 $\frac{3}{4}$	8	7
8. Length of alveolar series, lower jaw .....	?	10	9 $\frac{1}{16}$	10 $\frac{1}{8}$	9 $\frac{1}{2}$
9. Length of alveolar series, upper jaw ... ..	8 $\frac{3}{4}$	10 $\frac{1}{2}$	9 $\frac{7}{8}$	10.5	11 $\frac{1}{8}$ ?
10. Ratio of length of rostrum to total length of skull ...	.47	.48	.47	.46	.48

A comparison of these measurements shows that my two crania are smaller than the Refsnaes and Stamford skulls, and larger than the Cambridge one, which is that of a rather younger animal than A or B.

The asymmetry which is characteristic of the genus is present in both skulls, particularly in the bones of the facial region, those on the right being larger than on the left.

The skull of A is larger than that of B, but the upper and lower jaws are smaller and the tooth-rows are shorter, indicating that though it was the larger animal, yet, owing either to immaturity or sex, or both, the masticatory apparatus was on a slightly smaller scale. This is supported by the relative size of the tooth-sockets. The largest in A's upper jaw is  $\frac{1}{3}\frac{1}{2}$  inch less in diameter than that of B, and the smaller sockets show a similar proportion. This difference is about the same in the sockets of the lower jaw measured longitudinally, but is not as great in their transverse diameters.

### *Sutures*

More of these are closed in B than in A. For example, the occipito-frontal is entirely separate in the latter but united in the former, and a similar condition exists in the parieto-temporal and others.

### *Temporal Fossa.*

The surface of this is convex above and behind, but concave below and in front; it is roughly square in outline except at its lower and anterior part, where the postorbital process of the frontal and the zygomatic process of the temporal make an angle which is more obtuse than usual. The continuation of the occipital ridge, which forms its upper and posterior boundary, does not form a parabolic curve as described by Reinhardt (1866, p. 197), but rather an angle which approximates to a right angle.

The other specimens of *Pseudorca* which I have examined show a more or less well-marked parabolic curve, as does Reinhardt's figure (1866, p. 197). Sir Richard Owen's figure (1846) corresponds in this particular with my specimens.

Reinhardt (1866, p. 197) states that the parietal bone forms the highest point in the skull, and this is also the condition in the other skulls which I have examined. In both A and B, however, the nasal bones appear to stand quite as high, if not higher, than the parietal bone, in this respect being slightly more like *Orcinus orca*.

The origins of the zygoma are present on the bodies of the malaræ.

Two ear bones were found in the earth from which the skulls had been removed. I have attached one to each skull.

The nasal bones are all four present. In A the right is 2 inches, the left  $2\frac{1}{2}$  inches from the occipital crest, while in B these measurements are  $2\frac{1}{2}$  and  $2\frac{3}{4}$  inches respectively.

Both Reinhardt's description (1866, p. 197) and the Cambridge specimen from Tasmania show a distance of 3 inches.

### *Rostrum.*

This is shorter than the rest of the skull, and is regularly tapering in form, with no narrowing at the notch in B and very little in A.

In most of the other specimens I have examined this narrowing is marked.

The breadth of the two premaxillæ, together with the groove containing the vomer, measured opposite the notch, is  $5\frac{1}{2}$  inches in A and 5 inches in B. The breadth of the two maxillæ at the same place is only 3 inches, so the relatively greater width of the premaxillæ, characteristic of *Pseudorca*, is well marked. The outer edge of the premaxillæ is straight in B and very slightly concave in A. The outer and inner edges are approximately parallel to within about 2 inches of the end.

This character appears to be variable, and whereas in young



animals the outer edge tends to be concave, in older ones the outer edge is straight and parallel with the inner. This is well shown in the old specimen at the College of Surgeons Museum.

The premaxillæ appear on the palate for a length of 5 inches. They do not bear any tooth-sockets; there is no trace of any rugosity on the upper anterior surface in either A or B. It occurs in some of the Tasmanian specimens, and is shown in Van Beneden and Gervais (1880, plate l.) from a specimen of Prof. Reinhardt's in the museum at Paris. R. C. S. 2983, the skull of a very old animal, does not show so much rugosity as the Cambridge skulls do, though these belong to comparatively young animals.

### *Maxillæ.*

The only maxilla which is complete is the right one of B, but in all four the tooth-sockets are of the same shape. Superficially they form a continuous groove, the septa only reaching about half-way up the sockets at the centre line, but rising to palate level along the outer and inner edges. Thus they form inverted V-shaped partitions between the sockets. Neither published figures nor other specimens show this feature, and Sir Richard Owen's woodcut does not indicate it, but he states that this part was restored.

Reinhardt (1866, p. 201) states that "the teeth are placed in deep sockets, which, both in the upper and lower jaw, are completely separated from each other through their whole extent, but that the hindmost two sockets may coalesce, whereas the sockets of the teeth of the killers are most frequently only imperfectly separated."

Van Beneden and Gervais (1880, p. 547) agree with this description of *Orca*. They say "les alvéoles sont le plus souvent en partie confondus dans une même gouttière mais qui laisse entre chaque dent des cloisons incomplètes."

This grooved condition is not present in the lower jaw of B, but it is well marked in that of A.

It does not appear to be present in the other specimens I have examined.

The tooth-line is  $9\frac{7}{8}$  inches long in A and slightly curved; in B it is  $10\frac{1}{2}$  inches and straight.

The maxillæ are not ossified to the frontals in either case.

The palatine bones are much broken, as are the pterygoids. I do not think anything can be said about the relative position of the latter as I was only able to place one portion in position.

### *Mandibles.*

These differ from each other considerably. In A the symphysis is not united, and is 3 inches long.

Each bone measures  $19\frac{1}{2}$  inches from the articular surface to the front end, and there are sockets for ten teeth on either side. The dental row is  $9\frac{1}{16}$  inches long.

The septa between the sockets are very incompletely developed,

particularly in front, where they consist of but little more than pilasters of bone on the outer and inner walls of the alveolar groove, with a bridging piece over the dental canal. Farther back the sockets are a little more complete.

Sir Richard Owen's woodcut shows a similar condition in sockets numbers 5, 6, and 7 on the left side of the lower jaw.

The vertical plane of the sockets is twisted outwards as it runs forward, so that the anterior teeth look upwards and outwards, the posterior ones being almost vertical.

In B the symphysis is firmly united and  $3\frac{5}{8}$  inches long; each half of the jaw measures  $20\frac{1}{4}$  inches, and there are sockets for 9 teeth on each side. They are all complete, but several open freely into the dental canal below. The tooth-row measures  $10\frac{1}{2}$  inches.

### Teeth.

The dental formula based on the sockets present is:—

$$\begin{array}{cc} \text{A, } \begin{array}{c} 8 \cdot 8 \\ 10 \cdot 10 \end{array} & \text{B, } \begin{array}{c} 8 \cdot 9 \\ 9 \cdot 9 \end{array} \end{array}$$

This formula varies considerably, as the following examples show:—

Van Beneden (1889, p. 69) gives

$$\begin{array}{cccccccc} 10 \cdot 10 & 10 \cdot 9 & 9 \cdot 9 & 9 \cdot 9 & 8 \cdot 8 & 11 \cdot 11 & 11 \cdot 11 \\ 10 \cdot 10 & 10 \cdot 10 & 10 \cdot 10 & 9 \cdot 9 & 10 \cdot 10 & 11 \cdot 11 & 12 \cdot 12 \end{array}$$

$$\text{R. C. S. 2987 is } \begin{array}{c} 8 \cdot 8 \\ 9 \cdot 10 \end{array}$$

$$\text{R. C. S. 2984 is } \begin{array}{c} 8 \cdot 8 \\ 8 \cdot 8 \end{array}$$

Fifty-four teeth are in my possession; some were given me by Mr. Phillips with the lower jaw of A.

The crowns are curved inward and conical; though some of the roots are nearly straight, others are much curved.

The enamel is of a light bluish-grey colour, and corresponds with Sir Richard Owen's description of the Stamford specimen. It is white in all the other specimens I have seen, so presumably the grey colour is due to the action of the peat.

At the neck the colour changes to cream and the roots are light yellowish brown, much the same as the bones.

The crowns are not much worn, but several show grooves on the lower part just above the neck, caused doubtless by the rubbing of opposing teeth.

The roots in many cases are flattened on one or more surfaces, and in some even hollowed or fluted, so that a section is kidney-shaped.

Where the hollowed surface occurs it is probably the posterior, for in Van Beneden and Gervais (1880, plate xlix. 4 c, *Orea*) it is shown as such. In addition, the teeth would fit in the jaw best that way, taking into consideration the worn surfaces due to opposing teeth.

Two of the teeth given me by Mr. Phillips show extreme flattening on the sides, as proved by the sockets they fit. They are small; one of them is the hindmost of the right side of the lower jaw of A.

Sir William Flower (1883, p. 507) describes the teeth of *Pseudorca* as cylindrical, and I think the teeth of my specimens are rather more like those of *Orcinus orca* than the ones which have been previously described. Many of them show a neck.

The roots are closed in most cases, but some of the larger ones have an opening  $\frac{1}{8}$  to  $\frac{1}{4}$  of an inch in diameter. This corresponds with Reinhardt's (1866) description, p. 201.

The circumference of the largest tooth is  $3\frac{3}{4}$  inches and its length  $3\frac{7}{16}$  inches. The circumference of the crown is  $2\frac{3}{4}$  inches. These are all larger than those described by Reinhardt (1866) or Sir Richard Owen (1846).

### Vomer.

This bone appears on the palate to about the same extent as in Sir Richard Owen's figure and in the Middelfart and Refsnaes specimens described by Reinhardt, but it shows more than in the figure (plate I.) of Van Beneden and Gervais (1880). It was much broken in A and B, and though I have fitted the halves of the rostrum as closely as I could, there may be a little too much of the vomer visible.

### Vertebrae.

The numbers present appear to be:—

In A: cervical 7, dorsal 10, lumbar 10, caudal 17, some missing.

In B: „ 7, „ 10, „ 11, „ 18, „ „

Other specimens give:—

R. C. S. 2983 = c. 7, d. 10, l. 9, ca. 23.

R. C. S. 2984 = c. 7, d. 10, l. 9, ca. 21.

Reinhardt 1866 = c. 7, d. 10 or 11, l. 9, ca. 21.

A portion of the series was got under such conditions that it was reasonably certain they were in their proper sequence. These were strung together, and remain so still. Though there was some mixing of the bones, it was not very difficult to arrange the vertebrae in a graduated series based on size and shape.

The atlas was allocated by its fitting on the occipital condyles, that of A being slightly the larger. The arrangement was tested by the number of epiphyses ossified to the centra, which was found to be greater in B than A. It included the known series of vertebrae which were 2nd lumbar to the end in A, and the posterior point of transition from separate to ossified epiphyses was included in these. This corresponded with the state of ossification of the skull and jaw of A, and so made it pretty certain which specimen belonged to each skull.

*Cervical Vertebrae.*

In A the first six of these are ankylosed, both by their bodies and spinous processes, forming a single bony mass.

The arches are incompletely developed at the sides, forming incomplete canals for the exit of the spinal nerves.

The transverse process of the axis is small, corresponding with Reinhardt's (1866, p. 206) description, while that of the atlas is large and thick.

The seventh cervical is quite free from the other vertebrae. It has a long transverse process and two articular facets on the body.

Van Beneden (1880, p. 550) states "son corps ne fournit pas de facette costale apparente."

In B the first five bodies and spinous processes are fused, the neural arches being more complete than in A.

The sixth and seventh are ossified together, and the transverse process of the seventh is not so long as in A. Two articular facets are present on the body, but they are not quite so large as in A.

The condition as to fusion in some other skeletons is:—

R. C. S. 2983 ...	1-6 fused.
R. C. S. 2984 ...	1-5 "
British Museum	1-6 "
Cambridge .....	1-4 "

The British Museum specimen has a costal facet on the right side only.

*Dorsal Vertebrae.*

These correspond generally with Reinhardt's description, and are ten in number (possibly eleven in A).

The bodies increase in length from  $1\frac{3}{8}$  inches to 4 inches in A, and  $1\frac{3}{4}$  inches to  $3\frac{5}{8}$  inches in B.

The series is about 28 inches long in A and 27 inches in B, not allowing anything for the intervertebral fibro-cartilages. The first dorsal is  $1\frac{1}{2}$  times the length of the seventh cervical. Reinhardt (1866, p. 207) states that the first dorsal is scarcely longer than the last cervical.

In A the posterior epiphysis of the second dorsal is the first to be free from the body. In B the anterior epiphysis of D7 is the first not ankylosed.

In A the mamillary process can be distinguished from the anterior articular process, from the second to the seventh vertebra inclusive, and I think it can be made out in the eighth to a slight extent. In the last two it appears to be the mamillary which persists.

In B, however, this division is hardly to be made out in front of the third, and is very indefinite or absent from the sixth back.

In both specimens the posterior articular process does not occur behind the sixth, and the anterior articular process does not clasp the spinous process further back than this.

Reinhardt gives this point as the seventh in the Middelfart specimen and sixth in Refsnaes.

The transverse processes increase in length from before backwards, and in A that of the tenth on the left side is thinner and more like that of a lumbar vertebra.

There is a small spine on both sides of the body of the sixth vertebra of both A and B. It is situated where the costal facet would be.

This spine is smallest on the left side of A and very large on the left of B. There is a corresponding ridge and spine pointing inwards and forwards on the under surface of the transverse processes of both seventh dorsal vertebrae. It is not visible on the left of B as it has been chopped off, but I think that the damaged part indicates its former existence.

Reinhardt (1866, p. 208) found the condition in the Middelfart specimen, and described it as a vestige of the head of the seventh rib.

The ridge is present on the under surface of the transverse process of the seventh dorsal vertebra of the Cambridge skeleton, but there is no spine at the site of the costal facet.

There is one epiphysial disc for which I cannot find a place. It is of such a size and shape that it would fit a dorsal vertebra somewhere between the third and sixth; consequently it must belong to A, as in B these are united to the bodies. If this is so, A should have eleven dorsal vertebrae.

We shall see that B has one more lumbar vertebra than A; and if A had one more dorsal than B, it would make the totals the same.

If there is one dorsal vertebra lost, A would have had eleven like Reinhardt's Middelfart specimen. I have, however, not reckoned this missing vertebra in numbering the vertebrae.

I have made inquiries, but can find no trace of it, and we certainly examined the site very carefully.

The ventral surfaces of the bodies become somewhat ridged in the posterior vertebrae, forming a gradual transition to the keeled condition in the lumbar region.

#### *Lumbar Vertebrae.*

In A there are ten and in B eleven. Their characters appear to be as described by Reinhardt, but the forward inclination of the transverse processes continue as far back as the sixth.

An exception is No. 2 of A, in which they make a right angle with the longitudinal axis.

#### *Caudal Vertebrae.*

I have considered the last lumbar to be the most anterior of those bearing a bifurcation of the posterior part of the ventral keel on the body, and the first caudal to be the one next behind this, which also in both A and B is the first to have a perforation of the root of the transverse process for the passage of the dorsal

branch of the caudal artery. This foramen is much smaller in the second of A than in others.

These vertebræ form a gradually diminishing series, and at the 16th in B the major diameter suddenly changes from the vertical to the transverse where the tail fin commenced.

In both A and B, 18 caudal vertebræ were found. In A, however, I think numbers 13, 14, and 15 missing, so the last vertebra present is the 21st, whereas in B the last is the 18th.

The terminal vertebræ are missing, though we searched the earth in the situation of the tails very carefully.

The anterior articular processes disappear after the ninth in A and the seventh in B. Reinhardt (1866, p. 212) gives this as the fifth.

The last vertebra to bear anything resembling a transverse process is the eighth in A and tenth in B. Where this has disappeared there is a vertical canal through the side of the body.

The respective lengths of the skeletons, excluding soft parts, is made up as follows:—

A.			B.		
	ft.	in.		ft.	in.
Vertebræ and skull.....	13	7	Vertebræ and skull...	13	9
Caudal 13, 14, 15 missing	0	6	Six terminal vertebræ		
„ terminal „	0	2	missing.....	0	4½
	14	3		14	1½

#### *Chevron Bones.*

Sixteen of these were found, so that half the number is missing. They correspond with Reinhardt's description; in one the lateral halves are separate.

#### *Ribs.*

Parts of thirty-nine were found. Most are fairly complete, but they were very fragile and difficult to get out of the clay.

The first six ribs have both a head and a tubercle, the others a tubercle only.

Text-figure 1.



Probably a rudimentary rib.

The first pair are very broad, the second transitional, and in fact they correspond with Reinhardt's description.

Twenty sternal ribs were found, so that not many are missing. There are three slender anterior ribs.

In A six pairs have heads for articulation with the five pairs of notches in the sternum, two articulating with each side of the fourth segment. In B one is missing, but fragments indicate that the arrangement is probably the same as in A.

There is a fragment which appears to be that of a rib. It is smaller than any of the others, and of somewhat different shape. It has only one head, but there is a flat projection on the posterior border  $\frac{3}{4}$  inch from the head which somewhat resembles the process for articulation with the next transverse process as seen in *Platanista*.

### *Sternum.*

In A this consists of four segments; the two anterior only are ankylosed. The greatest width is  $7\frac{1}{2}$  inches and length 18 inches.

The perforation in the manubrium extends to the anterior end, so that it has the form of an elongated notch. There is the appearance, however, that the open end was filled in with cartilage.

In B only three segments were found, and all are firmly united. Apparently, however, the fourth segment was free.

The greatest width is  $5\frac{1}{2}$  inches and length 15 inches, to which should be added about 2 inches for the fourth segment.

The perforation is completely surrounded by bone and is smaller than in A.

### *Hyoid.*

In A this consists of five pieces. The basi-hyal is a T-shaped bone showing two cratered projections at the front end of the central piece for the cartilaginous attachment of the stylo-hyals, while the thyro-hyals were joined to the lateral projections, forming with them a crescent. All bones were joined by cartilage.

In B the basi-hyal and thyro-hyals are ossified together, forming a crescentic short-stemmed T. The stylo-hyals were united to basi-hyal as in A.

The hyoid bones of A are distinctly larger than B, but the maximum spread is the same, viz.  $10\frac{1}{4}$  inches.

### *Scapulae.*

The two scapulae got out by the workmen were much broken, but the others are in fairly good condition; fortunately one belongs to each individual.

In A the glenoid cavities are  $2\frac{5}{16}$  inches in greatest diameter. The maximum length is  $12\frac{3}{4}$  inches, and height  $8\frac{5}{8}$  inches. The ridges for the attachment of muscles are poorly marked, and the supraspinous fossa is quite narrow,  $\frac{3}{8}$  inch wide.

In B the glenoid cavities are  $2\frac{1}{2}$  inches in diameter, and the length and height are  $12\frac{1}{2}$  and  $8\frac{7}{8}$  inches respectively.

The bone is a little denser than in A and the supraspinous fossa a little wider.

The acromion and coracoid processes in the left scapula of B, in which alone they are uninjured, show a roughened margin, as do the upper borders where they are present. These processes appear broader than those of the British Museum and Cambridge skeletons, but these are less mature.

### *Humerus.*

These bones are massive and just under 5 inches long, measured from the tuberosity to the lower articular surface.

The tuberosity shows a smooth surface as though it articulated. All four are similar and in very good condition.

### *Radius and Ulna.*

The first is about  $5\frac{1}{2}$  inches long,  $\frac{1}{2}$  inch longer than the humerus. The ulna is  $4\frac{5}{8}$  inches long and the olecranon process well marked. It is ossified to the shaft.

(Gray (1866, p. 290) states that the ulna is nearly twice the length of the humerus.

The lower epiphyses of the ulnæ are more firmly ossified to their shafts than those of the radii, which are broken away in places.

The humeri, radii, and ulnæ of A are very much like those of B, and I do not think it is possible to distinguish them with certainty.

### *Carpus.*

Nine carpal bones were found. They are all flattened on their outer and inner surface, and show no articular facets.

### *Manus.*

Sixteen phalanges were found; none are terminal, and all bear evidence at the ends of incomplete ossification. They were scattered, several lying under one of the scapulæ.

In conclusion, it would appear that these two skeletons were deposited in one of the head-waters of the Wash at some time since the early Neolithic, and before the Roman period. They may belong to the same school as the type-specimen of the genus, which is lost, and although they show some differences from the specimens which have come from the sea in recent years, yet these differences are probably not sufficient to be considered specific. Perhaps the most remarkable variation is that of the teeth and tooth-sockets, which are both somewhat like those of *Orcinus orca*; but the fact that the condition of the sockets is



very different in the lower jaws of these two animals, which lay side by side and are otherwise so similar, must make one hesitate before attaching any specific value to such variation.

I am very much indebted to the following gentlemen for their kind help and encouragement, without which it would have been impossible to write this description:—Mr. R. F. Aubrey, Mr. R. H. Burne, Mr. Forster-Cooper, Sir Sidney Harmer, Prof. Marr, and Mr. Phillips.

I have given specimen A to the Museum of Zoology, Cambridge University, and specimen B to the British Museum (Natural History).

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Skull of specimen B from below, showing alveolar groove.  
2. The same from above.

## PLATE II.

- Fig. 1. Skull of B from the right side, showing height of nasal bones and shape of temporal fossa.  
2. Upper view of mandible of B, complete tooth sockets are seen.

## PLATE III.

- Fig. 1. Scapulæ of A and B with corresponding humeri, radii, and ulnæ; one ulna is the natural colour. The large size of the acromion and coracoid processes is seen.  
2. Sternum of B. The fourth segment is missing.  
3. Sternum of A. The perforation in the manubrium is incomplete.



8. Further Observations on the Myology of the Pectoral Region in Fishes. By E. W. SHANN, B.Sc., Ph.D., F.Z.S., Biology Master at Oundle School.

(Text-figures 1-4.)

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I. Introduction.

II. The Myology of the Pectoral Region in *Lepidosiren* and *Polypterus*.

1. The Lateral Muscle.
2. The Pectoral Girdle.
3. The Pectoral Fin.

III. The Cleithro-hyoideus Muscle in the Teleostei.

IV. The Degrees of Homology between the Muscles of the Pectoral Region in various Orders of Fishes and in Urodele Batrachians (with Key).

I. INTRODUCTION.

The following observations are supplemental to two previous papers on the myology of fishes: the first, "On the Nature of the Lateral Muscle in Teleostei" (Proc. Zool. Soc. 1914), paved the way for the second, "The Comparative Myology of the Shoulder Girdle and Pectoral Fin of Fishes" (Trans. Roy. Soc. Edinburgh, 1919). The notes and drawings for this latter work were made before the war, and at the date of their publication I had neither the time nor the opportunity to complete the programme which I had undertaken. The Dipnoi were left untouched, and though figures of *Polypterus* were drawn they were not described. Moreover, beyond a Key to the comparative myology, no general conclusions were arrived at. The monograph, however, incomplete as it admittedly was, led to interesting correspondence with other workers both at home and abroad. Stimulated by this, and at the instance of my friend Prof. D. M. S. Watson, F.R.S., F.Z.S., on the first available opportunity I resumed my studies at the point where they had been relinquished. I am indebted to Prof. Graham Kerr, F.R.S., F.Z.S., for the specimens of *Lepidosiren* and *Polypterus* upon which my observations are based.

II. THE MYOLOGY OF THE PECTORAL REGION IN *LEPIDOSIREN* AND *POLYPTERUS*.

1. The Lateral Muscle.

The composition of the lateral muscle of the other Osteichthyes conforms closely with that of the Teleostei, consisting of four series of hollow cones, two above and two below the lateral line. In the pectoral region four areas can still be traced; of

these, the two dorsal are completely severed from the two ventral by the passage of the horizontal septum which runs from beneath the lateral line to the vertebræ. There are no "red fibres" in connection with the lateral line.

#### LEPIDOSIREN.

In *Lepidosiren* several peculiarities of the lateral muscle are worthy of special consideration.

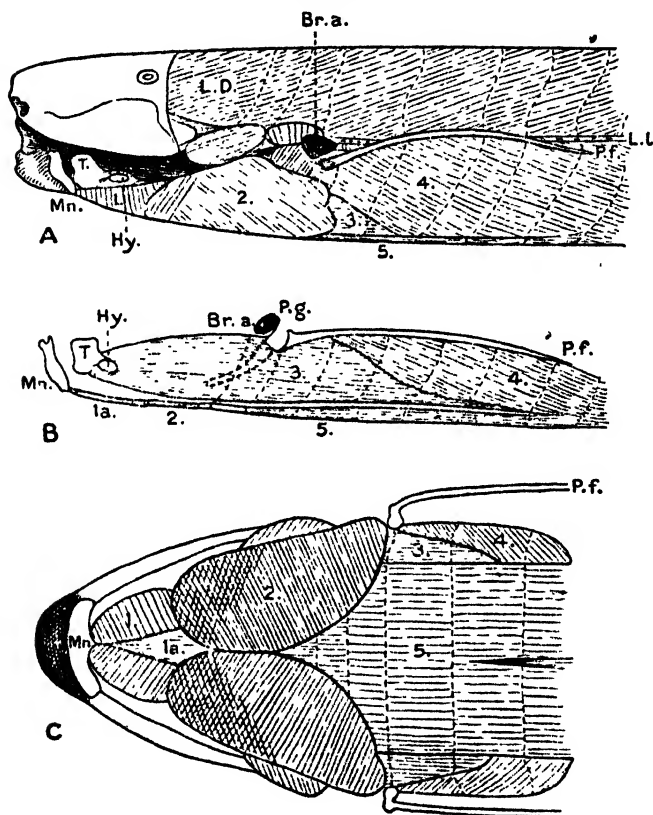
The general arrangement of the lateral muscle behind the pectoral girdle closely resembles that of *Polypterus*, except for the greater thickness of the ventral body-wall. This resemblance may be due in part to the fusiform shape of the body which is shared by both forms. At the same time it differs widely from the condition which has been described in a fusiform Teleostean, namely, *Conger*. In these presumably primitive forms the myomeres remain more nearly in juxtaposition to the vertebræ which bear them; or, in other words, they form very much shallower cones than are found in the Teleost myomeres. The dorsal posteriorly directed cones, large in *Polypterus*, in *Lepidosiren* so far preponderate as entirely to exclude the smaller anteriorly directed cones from appearing at the surface. Owing to the great thickness of the abdominal wall the conical structure of the ventral moiety is retained almost as far forward as the pectoral girdle. A very thick fascia separates the dorsal from the ventral moiety.

The superficial divisions of the lateral muscle of *Lepidosiren* are illustrated in text-fig. 1. In the side view (A) the latero-dorsal portion is seen as a massive muscle whose fibres slope rather steeply from below anteriorly to above posteriorly; it has a very extended origin upon the whole side of the skull as far forward as the eye. The ventral moiety anterior to the tip of the pectoral fin is divided by distinct fasciæ into superficial areas as well as into layers. The superficial areas are numbered similarly in each of the drawings A, B, and C; of these areas 4 is considered to be the latero-ventral portion, the remainder derivatives of the mesio-ventral portion.

On making a mid-ventral longitudinal incision (as in C, *mn.* to 5) a distinct fascia is found completely separating a thin outer layer from a thick inner layer. Following the incision posteriorly the fascia is found to disappear in the 6th myomere behind the base of the pectoral fin; here the fibres of 5 become confluent with those of 4. Dissecting from the mid-ventral line to the right (*i. e.* left of the animal) and then upwards the whole of 1, 1 *a*, 2, and 5 come away readily from the underlying part, 3. B shows the appearance of the left aspect after the superficial muscle layer has been removed; ventrally are seen the cut edges of 1 *a*, 2, and 5. I have not encountered this continuity of muscle from the mesio-ventral portion to the mandible in any other group of fishes.

Part 3 is a massive muscle taking origin on the hyoid and passing back beneath the pectoral fin to be inserted in part 4; the pectoral girdle is embedded in this muscle (where it is shown as by transparency in B), but there is no fascia to delimit a

Text-figure 1.

Lateral Muscle of *Lepidosiren* ( $\times \frac{1}{2}$ ).

A. Left aspect, superficial.

B. Left aspect, deeper layer.

C. Ventral aspect, superficial.

*Br.a.*, branchial aperture; *Hy.*, hyoid; *L.D.*, latero-dorsal portion; *L.I.*, lateral line; *Mn.*, mandible; *P.f.*, pectoral fin; *P.g.*, pectoral girdle; *T.*, tongue.  
1, 1a, 2, 3, 4, 5, parts of the ventral moiety of the lateral muscle.

cleithro-hyoideus such as is found in the vast majority of Osteichthyes. The parts 3 of either side are separated by a thin vertical septum near their origin, and a little further back become widely separated by the pericardium, of which they form

the lateral walls. Part 4 overlies part 3 to a certain extent, and its free edge can be dissected away from the portion of 3 which underlies it as far as the wavy line shown in B: at this level the fibres of parts 3 and 4 become intermixed. By the 7th myomere behind the base of the pectoral fin (one behind the tip of the fin) all trace of areas and layers is lost.

Parts 1, 1 $\alpha$ , and, to a great extent, 5, serve to depress the mandible. Part 3 serves to retract the hyoid and thus lower the tongue. Part 2 serves as a constrictor of the pharynx; its deeper fibres, especially in the forward area, run obliquely to the superficial ones (as shown in C); thus its power of enfolding the pharyngeal cavity is greatly increased.

#### POLYPTERUS.

Owing to the relative straightness of the myocommata in this form there is little external evidence upon which to define a mesio-dorsal from a latero-dorsal portion. The greater bulk of the dorsal moiety runs forward beneath the pectoral girdle to take origin on the occiput. In the pectoral region the greater part of the muscle, judging by the direction of its fibres, appears to belong to the latero-dorsal portion.

There is also below the lateral line very little distinction between the latero-ventral and the mesio-ventral portions.

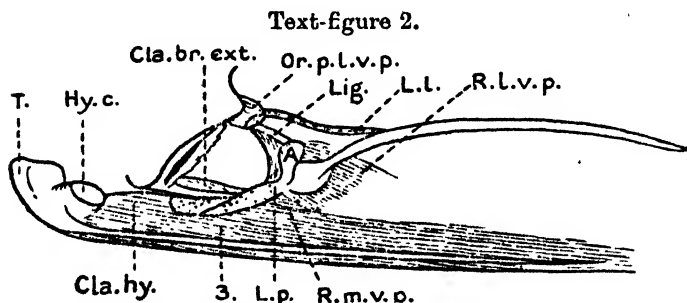
Internally, in the dorsal moiety, the upper posteriorly directed cones are so large as almost to obliterate the lower ones. (Owing to the position of the anus, the conical structure of the ventral moiety is practically non-existent; it is composed almost throughout its length of a single layer covering the abdominal cavity.)

### 2. The Pectoral Girdle.

#### LEPIDOSIREN.

The great reduction of the skeletal elements of the shoulder-girdle exhibited by *Lepidosiren* results in considerable departure from the normal distribution of the shoulder-muscles. No skeletal element occurs above the articular cartilage of the fin, the said cartilage being connected to the basi-occipital by a strong ligament (such as occurs in many Teleosts). No part of the dorsal moiety of the lateral muscle contributes to the fixation musculature of the girdle. The ventral symphysis, formed here by the clavicles, is embedded in the deeper layer of the mesio-ventral portion, as was noted above. In consequence of this it makes no appearance on the ventral surface, as is the case in almost all other fishes; and, as a further consequence, there is no retractor mesio-ventralis pectoralis inferior, nor any muscular connection between the girdle and the mandible. The general relations of the girdle to the lateral muscle are shown in text-fig. 1, while

text-fig. 2 illustrates the dispositions of the smaller muscles. Humphry\* has worked out the myology of *Ceratodus*, and the synonyms cited below refer to his observations on that type.



Shoulder Muscles of *Lepidosiren* (X 1).

Left aspect, after removal of constrictor muscles, and almost the entire mesio-ventral portion of left side. *A.*, articular cartilage (showing insertion of p.l.v.p.); *Hy.c.*, ceratohyal (cut); *Lig.*, ligament; *L.l.*, lateral line; *T.*, tongue. For other letters see text.

### (1) *The Posterior Muscles.*

- (a) Dorsal absent.
- (b) Retractor latero-ventralis pectoralis.
- (c) Retractor mesio-ventralis pectoralis.

(b) *Retractor latero-ventralis pectoralis* (r.l.-v.p.); *synon.* *Serratus*, Humphry:—

The muscle is part of that numbered 4 in text-fig. 1. It is a thin sheet traversed by myocommata, and is attached to the posterior border of the articular cartilage, as well as spreading, to a slight extent, upon the adductor muscle of the fin. Only the dorsal fibres of the latero-ventral portion (muscle 4) are inserted on the girdle, and may therefore be said to constitute the retractor; the muscle spreads ventrally to the fin over muscle 3, but it is no longer inserted on the girdle.

(c) *Retractor mesio-ventralis pectoralis* (r.m.-v.p.); *synon.* *Pectoralis* (and *Latissimus dorsi*?), Humphry.

By reference to text-fig. 1, B it will be seen that the whole girdle of either side is embedded in a mass of muscle numbered 3. The mass is derived from the mesio-ventral portion of the lateral muscle, though not comprising the whole of that portion, and those fibres which are attached to the posterior border of the girdle must function as retractors. At the same time there is no fascia to distinguish a definite retractor muscle from those parts of the same mass which run forward, externally to the girdle, to take origin on the ceratohyal.

\* "The Muscles of *Ceratodus*," *Journ. Anat. and Phys.* vi., 1872.



The r.m.-v.p. thus constituted takes origin from the whole posterior border of the girdle, underlying at its upper extremity the r.l.-v.p. described above.

The homology of this muscle is somewhat obscure, but it apparently represents in part the r.m.-v.p. sup. and med. of other fishes. The r.m.-v.p. inf. is undoubtedly wanting in *Lepidosiren*.

## (2) *The Anterior Muscles.*

- (a) Dorsal wanting.
- (b) Protractor latero-ventralis pectoralis.
- (c) Muscles derived from the mesio-ventral portion :
  - (i.) Levator pectoralis.
  - (ii.) Cleithro-branchiales.
  - (iii.) Claviculo-hyoidens.

(b) *Protractor latero-ventralis pectoralis* (p.l.-v.p.); synon. Trapezinus, Humphry :—

This is a small muscle which runs from its origin on the basi-occipital, parallel to the ligament mentioned above, to its insertion on the anterior outer border of the articular cartilage. Its tendinous insertion is in part continuous with that of the r.l.-v.p. over the outer surface of the articular cartilage; further, since the fibres of the two muscles also take the same direction, there can be little doubt that they belong to the same portion of the lateral muscle.

(c) Muscles derived from the mesio-ventral portion :

- (i.) *Levator pectoralis* (l.p.); synon. Sterno-cleidomastoideus, Humphry :—

This muscle is represented by a very slender plate of fibres which forms the posterior rim of the branchial chamber. From its origin on the basi-occipital, immediately beneath the protractor, it runs almost vertically downwards to be inserted on the inner border of the cleithrum. Some of the anterior fibres, bending sharply forward near their insertion, extend beneath the origins of the cleithro-branchiales.

- (ii.) *Cleithro-branchialis externus* (cli.-br.ext.) :—

A small, but well-defined, strap of muscle taking origin from the inner upper surface of the cleithrum and passing forwards to be inserted on the lower posterior rim of the second branchial cartilage. Beneath this lies a smaller, but nevertheless distinct, muscle which runs to the lower posterior rim of the third branchial cartilage; this constitutes the cleithro-branchialis internus.

The cleithro-branchiales thus differ in their mode of insertion from the condition to be observed in all other groups of the Osteichthes. This may be due in part to the extreme reduction of the branchial skeleton in general and of the two posterior arches in particular; at the same time it suggests an arrangement

more nearly akin to the segmental plan of the generalised fish type such as occurs in existing Elasmobranchs.

(iii.) *Claviculo-hyoideus* (cla.-hy.); synon. *Coraco-hyoideus*, Humphry :—

Taking origin on the swollen ventral extremity of the ceratonyal, the whole of whose posterior circumference it grips, a stout muscle runs directly backwards, expanding laterally as it goes. This muscle is illustrated in text-fig. 1, where it is denominated 3, and in the context its insertion is fully discussed. The innermost fibres run to the pectoral girdle where they are inserted into its outer surface, both into the clavicle and the cleithrum. These fibres constitute the claviculo-hyoideus, as shown in text-fig. 2 (*cla.hy.*); it is clear, however, that they are in no way delimited from the remaining fibres of muscle 3, although they are separated by a tolerably distinct fascia from their fellows of the opposite side.

The clavico-hyoideus of *Lepidosiren* is not readily comparable with that of the Chondrostei or with the cleithro-hyoideus of other Osteichthes. In few other fish known to me does any portion of the muscle which runs from the hyoid arch to the pectoral girdle pass that structure and become directly confluent with the ventral body-wall. The condition is certainly not to be regarded as primitive, for it finds no parallel in the Chondrichthes. On the other hand, it cannot entirely be attributed to the reduction of the shoulder-girdle, the lower half of which (especially the ventral symphysis) is not nearly so reduced as is the case in many other Osteichthes. We have here, in fact, an approach to the condition in the Amphibia, where muscles completely invest the ventral aspect of the girdle, so that none of its skeletal parts appear beneath the skin (with the exception of the newly intercalated sternal elements).

#### POLYPTERUS.

##### (1) *The Posterior Muscles.*

- (a) Retractor dorsalis pectoralis.
- (b) Retractor latero-ventralis pectoralis.
- (c) Retractor mesio-ventralis pectoralis :
  - (i.) superior.
  - (ii.) medius.
  - (iii.) inferior.

(a) *Retractor dorsalis pectoralis* (R.d.p.):—

The great mass of the dorsal moiety runs forward beneath the girdle to be inserted on the skull, but a few of the superficial fibres are inserted into the inner aspect of the supracleivale and, to a less extent, of the cleithrum. These fibres constitute a retractor muscle; and since there is no distinct division between the mesio-dorsal and latero-dorsal portions, it seems well to designate it simply "retractor dorsalis pectoralis." It is illus-

trated in text-fig. 3, B, but the main point of insertion is higher up than the termination of the index line.

(b) *Retractor latero-ventralis pectoralis* (r.l.-v.p.):—

A very few fibres from the latero-ventral portion succeed in reaching the girdle immediately below the lateral line, where they are attached to the inner aspect of the lower postclavicle.

(c) *Retractor mesio-ventralis pectoralis*:

(i.) *Superior* (R.m.-v.p.sup.):—

This muscle is clearly shown in text-fig. 3, B; it is not attached, as might appear to be the case, to the lower postclavicle, but runs beneath that bone to be inserted on the inner aspect of the cleithrum.

(ii.) *Medius*:—

Does not appear in either of the illustrations, but it may be defined as that section of the mesio-ventral portion which occupies the axil of the fin. It ends in the fascia which covers the adductor muscles of the fin. It is not clearly defined, however, either from the "superior" or the "inferior" section.

(iii.) *Inferior* (R.m.-v.p.inf.):—

As is seen in text-fig. 3, A, this is the only one of the series of retractors which is not traversed by myocommata right up to its point of insertion. The muscle is thin and is attached throughout its depth to the posterior rim of the cleithrum. The l.m.-v.p.inf. of either side are separated from one another by a marked septum in the mid-ventral line.

(2) *The Anterior Muscles.*

(a & b) *Protractor pectoralis.*

(i.) *Anterior.*

(ii.) *Posterior.*

(c) *Muscles derived from the mesio-ventral portion:*

(i.) *Levator pectoralis.*

(ii.) *Cleithro-branchiales.*

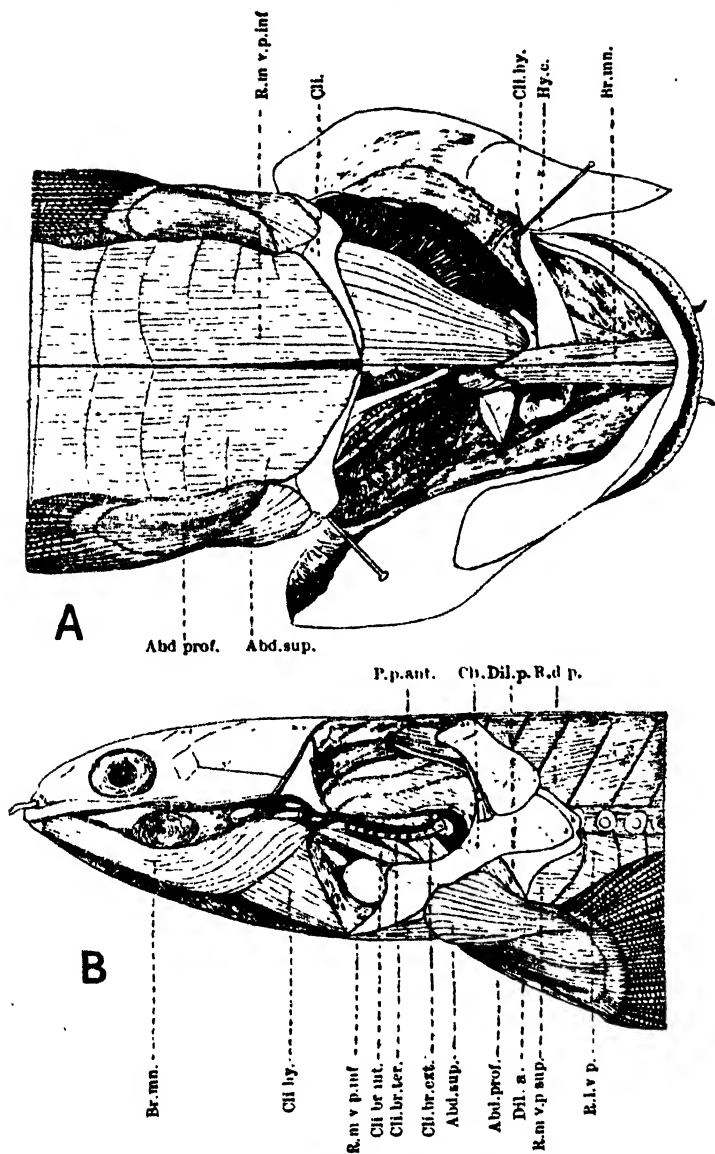
(iii.) *Cleithro-hyoideus.*

(a & b) *Protractor pectoralis anterior* (P.p.ant.):—

This is a short compact muscle running from the otic region of the skull to the inner aspect of the supraclavicle; it is seen in text-fig. 3, B. Beneath it lies a smaller muscle which I propose to call the protractor pectoralis posterior.

From the nature of their origins and insertions as well as from their functions, these two muscles appear to be homologous with the similar pair which occur in all Osteichthyes. At the same time it is worthy of note that they appear, from their position high above the lateral line, to be derivatives of the dorsal moiety (a) rather than of the latero-ventral portion (b); in the absence

Text-figure 3.

Pectoral musculature of *Polypterus* ( $\times 1$ ).

- A. Ventral aspect, after removal of constrictors. B. Left lateral aspect.  
*Br.mn.*, Branchio-mandibularis; *Cli.*, Cleithrum; *Hy.c.*, Ceratohyal.  
 Muscles as in text.

of developmental evidence, however, it does not appear to be justifiable to alter the nomenclature on this account.

(c) Muscles derived from the mesio-ventral portion :

(i.) *Levator pectoralis* :—

A cylindrical muscle running from the basioccipital to the inner upper aspect of the cleithrum. It does not appear in text-fig. 3, B, being hidden by the suprabranchial constrictors ; it runs parallel with the ligament (shown in the illustration as a white streak immediately above the constrictors), and just ventral to it.

By reason of its direction it functions rather as an additional protractor than as a levator, but, from its general topography, there can be little doubt of its homology with the levator pectoralis of Teleosteans.

(ii.) *Cleithro-branchiales* (Cli.-br.) :—

I find three distinct parts of this muscle which, arising close together on the inner aspect of the cleithrum, run as follows (see text-fig. 3, B) :—

(a) *Externus*, a short broad strap running almost vertically to the last ceratobranchial, just below the bend of that structure.

(b) *Internus*, a cylindrical muscle taking origin inside the above and running obliquely forwards to the ventral extremity of the last ceratobranchial.

(c) *Tertius*, a smaller cylindrical muscle lying between the two foregoing.

I have lately had some correspondence with Prof. D. M. S. Watson about the cleithro-branchiales of *Polypterus*. Prof. Watson found that on one side of his specimen this muscle formed a single continuous sheet, while on the other it was divided into two distinct bundles. In the two specimens of *P. senegalus* dissected by me, and on both sides of them, I found the same arrangement of the cleithro-branchiales which I have already illustrated and described. I therefore propose to retain my original description, though it is quite possible that a certain amount of variation occurs.

(iii.) *Cleithro-hyoideus* (clo.-hy.) :—

A powerful muscle, devoid of myocommata, which, arising from the anterior face of the lower third of the cleithrum, runs forwards to be inserted on the base of the hyoid arch. It is enclosed ventrally by the clavicle, but sends no fibres to that structure. In the mid-ventral line it is contiguous with its fellow of the opposite side, from which, however, it is separated by a fascia throughout its depth.

### 3. The Pectoral Fin.

#### LEPIDOSIREN.

Owing to the extreme reduction of the pectoral fin in *Lepidosiren* the muscles are excessively small and simple. The adductor

on the inner surface and the abductor on the outer each consists of a single compact bunch of fibres which, taking origin on the articular cartilage, is inserted on the basal cutilage of the fin. I can find no trace of muscular tissue between the segments of the fin-axis.

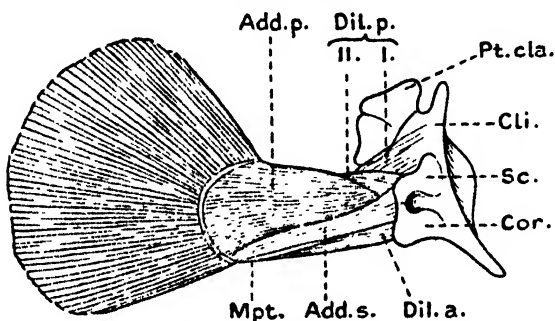
### POLYPTERUS.

#### (1) *Adductor*.

##### (i.) *Adductor superficialis* (Add.s.):—

A narrow strap-like muscle which takes origin on the anterior border of the scapula, and, in part also, of the coracoid. It runs

Text-figure 4.



Inner aspect of left pectoral fin of *Polypterus* ( $\times 2$ ).

Cli., Cleithrum; Cor., Coracoid; Mpt., Metapterygium; Pt.cla., Postclavicle (the index line runs to the upper); Sc., Scapula. Muscles as in text.

obliquely downwards to be inserted on the metapterygial radial, giving off a few fibres to the inner border of the metapterygium.

This muscle functions as a dilator rather than as an adductor; but it evidently corresponds to the add.s. of Teleosteans, which, in many cases, is also very small and only partially covers the add.p.

##### (ii.) *Adductor profundus* (Add.p.):—

The largest muscle of the adductor series, arises at the junction of the scapula and coracoid, and spreads fan-wise, gathering fibres from the fascia covering the Dil.p.ii., from the mesopterygial cartilage, and from the metapterygium, till it covers the whole distal area of the inner surface of the fin. At their extremity the fibres pass into a tendinous sheet which is inserted on the bases of the lepidotrichia. Some of the deeper fibres of this muscle run obliquely (about 60 degrees) to those seen on the surface; there is no fascia, however, between the two sets of fibres.

##### (iii.) *Dilator posterior* (Dil.p.):—

From the fact that this muscle takes origin behind the glenoid border it evidently belongs to the adductor series. It agrees

in position, moreover, with the dilator posterior which occurs in many Teleosteans, but differs from any such known to me in that it is divided into two parts (designated i. and ii. in text-fig. 4).

Part i. is a triangular muscle which takes origin on the inner aspect of the cleithrum immediately above the centre of the scapula, whence its fibres run obliquely downwards to their insertion on the upper border of the propterygium; a number of the dorsalmost fibres, however, become collected into a tendon which, after forming the upper rim of the fin musculature, becomes inserted on the propterygial radial. This muscle is also partly visible from the outside of the fin, as appears in text-fig. 3, B.

Part ii. has the shape of a flattened cone which, taking origin at its base on the upper posterior border of the scapula, dives beneath the adductor profundus to its insertion along the inner border of the propterygium.

These muscles serve to keep the upper supports of the fin taut, and so to dilate the fin, during the back stroke induced by the adductor profundus.

## (2) *Abductor*.

### (i.) *Abductor superficialis* (Abd.sup.):—

This and the other muscles of the abductor series are illustrated in text-fig. 3. Abd.sup. is a thin sheet of muscle having an extensive origin on the outer aspect of the cleithrum. Owing to the fact that its fibres are inserted on the fascia which covers the adductor profundus, only a small portion of the muscle, and this in the dorsal region, reaches the distal area of the fin; no part of it, however, comes in direct contact with the fin skeleton.

### (ii.) *Abductor profundus* (Abd.prof.):—

Arising from the outer angle between the scapula and the cleithrum this large muscle spreads fan-wise, being augmented by contributions from the outer aspects of the propterygium, of the mesopterygial cartilage, and of the metapterygium. It ends in a tendinous sheet which is inserted on the bases of the lepidotrichia. As in the case of the adductor profundus, some of the deeper fibres run obliquely to those seen on the surface; again, however, there is no fascia between the two sets of fibres.

### (iii.) *Dilator anterior* (Dil.a.):—

This muscle takes the form of a slender cone which, arising at its basal end from the outer aspect of the coracoid, runs along the outer ventral border of the metapterygium on which its fibres are inserted. It forms the ventral border of the fin musculature, and is partly visible from the inner aspect (see text-fig. 4) as well as from the outer:

## III. THE CLEITHRO-HYOIDEUS MUSCLE IN THE TELEOSTEI.

*Cleithro-hyoideus*. Synon. Sterno-hyoid, Stannius, Vogt & Yung; Retractor hyoidei, Owen; Hyo-pectoralis, McMurrich; Hyo-clavicularis, Hamburger:—

A powerful muscle which forms the ventral border of the gill-chamber. It has a double origin on the cleithrum; the larger portion arises from the outer aspect of the cleithrum, usually in its lower third, while a smaller portion arises from the region of the symphysis, where it comes in contact with its fellow of the opposite side. The insertion occurs on the base of the hyoid arch. The muscle is usually much reduced in bulk as it approaches the point of insertion, but *Zeus* forms an exception.

In a few of the more specialised Teleostei a part of the cleithro-hyoideus runs from its insertion on the hyoid external to the cleithrum so as to become confluent with the muscle of the ventral body-wall (i.e. Retractor mesio-ventralis pectoralis inferior). This recalls the condition which we have observed in *Lepidosiren*; but in no Teleostean does the unattached outer portion of the muscle so far preponderate over the cleithro-hyoideus proper as is the case in the Dipnoan. Specialisation in this respect has apparently taken place along various lines, and those which have come to my notice in the course of these investigations will now be considered.

In most cases the ventral symphysis of the two cleithra is visible on removing the skin. In *Trigla gurnardus* a cylindrical muscle runs on either side of the ventral middle line from the urohyal to the symphysis of the cleithra. At the same time, another portion of the cleithro-hyoideus runs from the outer posterior border of the basihyal to the inner aspect of the cleithrum at the level of the origin of the cleithro-branchialis internus. Between these two portions a third is inserted on the basihyal and runs clear of the girdle, between the pectoral and pelvic fins (where it narrows considerably), to become confluent with the ventral body-wall. All three portions are separated from one another by fasciæ, and none show any trace of myocommata. A precisely similar condition was found in *Periophthalmus*.

In *Blennius pholis* the general disposition of the cleithro-hyoideus is similar to that in *Trigla*, but here the ventral portion of the cleithro-hyoideus proper is much more in evidence than the upper outer portion. In *Motella mustela*, on the other hand, conditions are reversed. The symphysis of the cleithra is scarcely visible, the ventral portion of the cleithro-hyoideus proper is reduced to a mere thread, and the outstanding feature on the ventral aspect is the large free portion. This upper portion differs from that in the foregoing types in that it arises on the level of the cleithro-branchialis externus and is inserted on the upper aspects of the uro- and basihyal; there is, moreover, no distinct fascia between it and the free portion.



In *Pholis gunnellus*, the symphysis is completely hidden by a muscle which runs direct from the urohyal to the rudimentary pelvic girdle. A large portion of the ventral muscle runs forward above the foregoing to be inserted on the posterior aspect of the basihyal; this represents the free portion of the cleithro-hyoideus, but differs from that of the above types in that it is traversed by myocommata. Above this again, but not separated from it by a definite fascia, is the cleithro-hyoideus proper.

#### IV. THE DEGREES OF HOMOLOGY BETWEEN THE MUSCLES OF THE PECTORAL REGION in various Orders of Fishes, and in Urodele Batrachians.

(References as in *op. cit.*, and not as in this communication.)

Attention was drawn in my previous paper (see Introduction) to the chaotic condition of the myological nomenclature of the pectoral region in Fishes, prior to my work. After perusal of the text, and particularly of the Keys to the musculature in Elasmobranchii and Teleostei, my observation will be found to be justified. In adopting a uniform system of nomenclature it was necessary to select one of two main lines of procedure: (a) to retain the existing names for muscles (giving precedence, in cases where two or more names had been applied to the same muscle, either to priority or to suitability), or (b) to introduce new names. After due consideration I decided to follow the latter course. This has led, in some cases, to the coinage of such cumbersome terminology as appears to demand an explanation; the explanation, moreover, involves the discussion of a wider subject, namely, the morphological value of the new nomenclature.

As a result of the investigations on the lateral muscle which were set forth in my previous papers, it was shown that a very considerable degree of similarity in the general build of the body exists in all the main Orders of living fishes. In the embryonic state the similarity is very much more marked than in the adult; but, even in the adult, at least behind the pectoral girdle, the lateral muscle retains a decided constancy of structure. The original metameric segmentation of the body muscle is maintained; and although the individual myomeres are bent into conical form they are still separated (right up to the pectoral girdle or, at all events, close up to it) by myocommata. The division of the lateral muscle by a horizontal septum beneath the lateral line, giving rise to a dorsal and a ventral moiety, is a constant morphological factor. Of more doubtful value, however, is the further subdivision of each moiety into a lateral and a mesial portion. It has been shown, for instance, that though the conical conformation of the lateral and mesial portions is fairly constant throughout the Chondrichthes on the one hand, and the Osteichthes on the other, yet between these two Sub-Classes certain discrepancies exist. The division of the moieties

into lateral and mesial portions is at best not very clearly defined, especially in the forward area with which we are chiefly concerned, and one cannot affirm that it has any true morphological value. At the same time, its use for descriptive purposes is beyond doubt, for it divides the lateral muscle behind the girdle into groups whose probable homology it would be difficult to deny (see Key at end of section). Though the term "latero-dorsal" is merely descriptive of relative position, for example, the term "Retractor latero-dorsalis pectoralis" is believed to imply a homologous muscle in the various Orders in which it occurs. The fact that the majority of the muscles attached to the pectoral girdle of fishes are merely fixation muscles, and not concerned with its actual movement, gives them a greater constancy of arrangement than is found in the higher Vertebrata. This constancy of arrangement first suggested to me the uniform system of nomenclature which I was led to adopt.

The special musculature of the pectoral girdle and fin in any given fish develops as a series of outgrowths from a definite number of myomeres, though, as Goodrich (38) has shown, the number of myomeres which commence the contribution in the embryonic stage may be considerably in advance of those which actually form the musculature of the adult (a certain definite proportion of the original muscle buds being discarded in the process of construction). The fact that muscles are developed from different embryonic myomeres in different groups of fishes does not necessarily imply that they are not homologous. As an extreme example of the argument one may cite the muscles of the pelvic fin in Teleostei; the homology of these muscles throughout the Order has never been questioned, and yet they may be developed from myomeres many places removed (*e. g.* in the Salmon and the Cod). Granted that homologous muscles are not necessarily derived from numerically homologous myomeres, it follows equally that we cannot look for them to be innervated by numerically homologous nerves. Thus, for the purposes of a general myological classification one is confined, to a large extent, to considerations of disposition and arrangement of parts. But there are degrees of homology, and the closer the relationship it is desired to show between the myology of any two types, the closer must be the attention paid to myomeric development and to innervation, both embryonic and adult.

The homologies suggested by similar names in my classification are of the broad general type which I have specified above. As a rough gauge of the degree of homology which is implied, I should suggest that it is comparable to that which exists between the pectoral myology of the Batrachia and the Reptilia, but it is not so close as that which exists between any two Orders of those Classes respectively. I regard the hiatus between living Fishes and Amphibians in respect of their pectoral musculature

as greater than that which exists between the latter and any other Class of Tetrapods. For this reason I have avoided the use of terms which are used in connection with Batrachian myology. At the same time, I have drawn attention to possible homologies which may exist between the muscles of the pectoral girdle in Fishes and certain of those exhibited by Urodele Batrachians.

Bearing in mind the foregoing proviso, we will proceed briefly to summarise the evidence collected on the various muscles of the pectoral region (cf. Key to the Comparative Myology of the Pectoral Region, at end of section).

### (1) *The Posterior Muscles.*

#### (a) *Retractor latero-dorsalis pectoralis* (R.l.-d.p.):—

Usually small and only slightly differentiated. In Batoids, however, it is well developed and devoid of myocommata. As a rule it is certain that the mesio-dorsal portion makes no contribution towards its formation; the Holocephali, however, form an exception to this statement, and for this reason the muscle has been named in that Order simply *Retractor dorsalis pectoralis* (R.d.p.). In the Holocephali, moreover, this and the succeeding muscles of the posterior series are more highly differentiated than in any other Order of living fishes.

It is possible that this muscle, after being rotated into a more vertical position, became the forerunner of the *Latissimus dorsi* of Urodeles. The origin from the dorsal element of the shoulder-girdle and the insertion on the dorsal portion of the body-musculature seem to suggest something deeper than a merely mechanical resemblance between these two muscles.

#### (b) *Retractor latero-ventralis pectoralis* (R.l.-v.p.):—

Usually small and slightly differentiated. Better developed in the Chondrichthes than in the Osteichthes. Attains its highest development in the Holocephali, where it is divided into two distinct sheets (*externus* and *internus*).

This muscle has been thought by Humphry and others to be homologous with the *Serratus* of Urodeles; a suggestion which, from the relative positions and proportionate sizes of the two muscles in question, seems quite possible.

#### (c) *Retractor mesio-ventralis pectoralis* (R.m.-v.p.).

##### (i.) *Superior*:—

Usually a large muscle which may or may not cover the foregoing. Except in the Holocephali, it is traversed by myocommata close up to its origin on the girdle.

This muscle, especially as represented by the Osteichthes, forms the lateral body-wall, and, almost undoubtedly, gave rise to the *Obliquus* of Urodeles. It is not actually divided into two superimposed layers, but, owing to retaining a trace of its conical formation, the deeper fibres run obliquely to the superficial.

(ii.) *Medius* :—

Only attains considerable development in the Chondrichthyes, while in all Orders of the Osteichthyes it is greatly reduced, and in the Chondrostei absent.

The R.m.v.p.med. is not represented in living members of the Batrachia. Its presence depends upon the occurrence of a very wide glenoid border, such as occurs in primitive fishes, but is gradually lost in the higher forms, while in living Batrachians it is reduced to a ball-and-socket joint.

(iii.) *Inferior* :—

Is almost invariably large and well defined, and frequently loses its myocommata before reaching the girdle. The curious exception presented by *Lepidosiren* is discussed in section II. of this paper.

This muscle forms the ventral body-wall, and Owen regarded its resemblance to the Rectus abdominis of the Batrachia as one of the surest homologies between the myology of that Class and of the Fishes.

(2) *The Anterior Muscles.*(a) *Protractor latero-dorsalis pectoralis* (P.l.-d.p.) :—

Is undeniably represented only in *Rhina* and the Rays. In the Holocephali a very definite protractor occurs in the region of the dorsal moiety; but, as it appears to be derived from the mesio-dorsal portion (in part) as well as from the latero-dorsal, it has been named Protractor dorsalis pectoralis (P.d.p.), cf. the corresponding retractor in the Holocephali.

It seems unlikely that a muscle which only appears in certain specialised Chondrichthoids should have a counterpart in the Batrachia. Nevertheless, the muscle designated "22" by Owen (73, fig. 140) corresponds as closely in position with the P.l.-d.p. as does that designated "11" (=latissimus dorsi) with the R.l.-d.p.

(b) *Protractor latero-ventralis pectoralis* (P.l.-v.p.) :—

The muscle is clearly defined throughout the Elasmobranchii, but is wanting in the Holocephali.

In the Osteichthyes the muscle, which I have there named Protractor pectoralis (P.p.), is divided with marked constancy throughout the Orders into two closely apposed portions (anterior and posterior). A question at once arises as to whether these two portions are not homologous respectively with the Protractors latero-dorsalis and latero-ventralis pectoralis of Elasmobranchs. This supposition, if correct, would simplify the classification; but the evidence is against its acceptance. In the Dipnoi and Chondrostei both protractors undoubtedly belong to the ventral moiety of the lateral muscle. In the Polypterini and in some

Teleostei, on the other hand, both protractors possibly belong to the dorsal moiety, judging by their position high up on the body. In the absence of developmental evidence I have not altered the nomenclature on this account, but I have compromised to the extent of using the term *Protractor pectoralis* (omitting the committal "latero-ventralis").

The *Protractor pectoralis* of *Osteichthyes* is very suggestive of the *Trapezius* (= *Protractor scapulae*, Owen) of *Urodela*, which is also divided into two parts, although these parts in the *Urodela* are more widely separated and more mobile.

(c) Muscles derived from the mesio-ventral portion.

(i.) *Levator pectoralis* (L.p.):—

Whether this muscle is actually derived from the latero-ventral or from the mesio-ventral portion would be difficult to affirm, and for that reason it has not been coupled with the term "mesio-ventral" in the nomenclature. In character and level of insertion it seems to correspond in many ways with the *Retractor mesio-ventralis pectoralis superior* (though always smaller in actual size); it has therefore been classified with the mesio-ventral derivatives. The main point is that in all Orders, except the *Chondrostei*, a well-defined muscle is found to run from the skull to the pectoral girdle at a level decidedly lower than the protractor muscles described above. In *Osteichthyes* the muscle is accompanied by a tendon, with which it may or may not be in actual contact. The relations of this tendon to the bones of the axial skeleton and of the pectoral girdle have been discussed under the heading "Teleostei."

It is possible that the *Levator pectoralis* of Fishes is the forerunner of the *Levator scapulae* of *Urodela*, but the latter differs in its origin, which is from the cervical vertebrae instead of from the skull.

(ii.) *Coraco-arcualis communis* (C.-a.c.):—

A specialised part of the ventral musculature only found in *Elasmobranchii*.

(iii.) *Coraco-branchiales*, etc.:—

In all fishes a muscular connection exists between the pectoral girdle and the branchial apparatus. There is, however, a very distinct difference in arrangement between the *Chondrichthyes* and the *Osteichthyes* in this respect.

In the *Chondrichthyes* we find a more or less distinct muscle bundle running from the coracoid to the base of each of the branchial arches. These bundles are known as the *coraco-branchiales* (C.br. 1-5).

In the majority of *Osteichthyes* muscle bundles run from the cleithrum to the posterior branchial arch only. These are known as the *Cleithro-branchiales* (Cli.br.). In *Chondrostei* there is but one such bundle. In *Teleostei* there are two, *externus* and

internus (the insertion of the latter is interna to that of the former, and its origin is higher up on the cleithrum). In Polypterini a third cleithro-branchialis occurs between the externus and the internus.

In *Lepidosiren* we find a somewhat intermediate condition between the Chondrichthyes and the remaining Osteichthyes. There are two cleithro-branchiales, and these are inserted on the second and third branchial cartilages respectively.

This element in the pectoral musculature of Fishes has no counterpart in the adult Urodele.

(iv.) *Coraco-hyoideus*, etc.:—

In all fishes a pair of contiguous muscles, one on either side of the median plane, runs from the pectoral girdle to the base of the hyoid arch. The muscles are named according to the skeletal element of the girdle from which they arise: thus, in the Chondrichthyes we have a Coraco-hyoideus (C.-hy.), in Dipnoi and Chondrostei a Claviculo-hyoideus (Cl.-hy.), and in Polypterini and Teleostei a Cleithro-hyoideus (Cli.-hy.).

The coraco-hyoideus of Elasmobranchii differs slightly from that of Holocephali in that it arises from the coraco-arcual septum instead of from the coracoid cartilage itself.

There can be little doubt that the Sterno-hyoid of Urodeles has been derived from this element of the pectoral musculature of Fishes, though, as one might expect, its relative size is much reduced.

It is interesting in this connection to find a "Pubohyoideus" (Owen) in the Salamander. This muscle, inserted on the hyoid and running back in the ventral body-wall till it reaches the pelvic girdle, vividly recalls the curious condition observed in connection with the claviculo-hyoideus of *Lepidosiren* and the cleithro-hyoideus of certain Teleosts where a "free portion" of the muscle runs back, external to the pectoral girdle, to become confluent with the ventral body-wall.

(v.) *Coraco-hyomandibularis* (C.-hm.):

A very specialised modification of the ventral musculature found only in *Raia* of the types examined, and probably confined to the Batoids.

(vi.) *Coraco-mandibularis* (C.-m.):—

A muscle highly developed in all Chondrichthyes. It is apparently wanting in the Osteichthyes with the possible exception of *Ceratodus*, for which Humphry (52) has described a "Genio-coracoid."

### (3) *The Fin Muscles.*

(a) *Adductor.*

The inner or upper musculature of the fin which serves to draw it in towards the side of the fish. With the exception of *Lepido-*

*siren* (in which the fin is so far degenerate as hardly to be comparable with that of any other of the types selected), the adductor muscle is divisible into two superimposed layers, superficialis (Add.sup.) and profundus (Add.prof.). The two layers are not very clearly defined from one another except in the *Polypterini* and *Teleostei*.

In *Polypterus* and in certain *Teleosteans* there is a third element of the adductor series, which has been described as *Dilator posterior* (Dil.p.).

(b) *Abductor*.

The outer or lower musculature of the fin which serves to draw it forwards away from the body. It is divided in a manner precisely similar to the adductor. Thus we have an abductor superficialis (Abd.sup.) and an abductor profundus (Abd.prof.); in *Lepidosiren* there is but one layer, while in *Polypterus* and in those *Teleosteans* which possess a dilator posterior we have, in addition, a dilator anterior (Dil.a.).

In certain *Teleosteans* whose pectoral fins have become modified for progression on a solid surface remarkable specialisation of the normally simple musculature occurs. The muscles of the pectoral fin of *Lophius* were described in some detail in this connection. Such cases, however, are rare, and do not detract from the value of a general nomenclature which is applicable to the vast majority of fish types.

There is at present no evidence upon which to base even the vaguest comparison between the myology of the fin of any known fish and that of the limb of any known *Batrachian*. Both start as a series of ventral buds from certain definite myomeres, but thenceforward each follows its own course in building the adult structure, and ontogeny offers as yet no clue to the phylogeny of the Tetrapod limb.

## KEY TO THE MYOLOGY OF THE PECTORAL REGION.

1. ELASMOBRANCHII. 2. HOLOCEPHALI.			3. DIPNOI. ( <i>Lepidosteus</i> .)	4. CHONDROSTEL 5. POLYPTERISI. ( <i>Polypeterng</i> .)	6. TELEOSTEI.	MODELA.
POSTERIOR MUSCLES.	(a) R.l.-d.p. (b) R.l.-v.p. (c) R.m.-v.p. (i.) sup. (ii.) med. (iii.) inf.	(a) R.d.p. (b) R.l.-v.p. (c) ext., (ii.) int. (d) R.m.-v.p. (i.) sup. (ii.) med. (iii.) inf.	(a) R.l.-d.p. (b) R.l.-v.p. (c) R.m.-v.p. (i.) sup. (ii.) med. (iii.) inf.	(a) R.l.-d.p. (b) R.l.-v.p. (c) R.m.-v.p. (i.) sup. (ii.) med. (iii.) inf.	(a) R.l.-d.p. (b) R.l.-v.p. (c) R.m.-v.p. (i.) sup. (ii.) med. (iii.) inf.	Latiss. dorsi. Serratus.  Obliquus. Rectus abd.
	(a) P.l.-d.p. (b) P.l.-v.p.	(a) P.d.p.	(b) P.p. (i.) ant. (ii.) post. (c) M.-V. (i.) L.p.	(b) P.p. (i.) ant. (ii.) post. (c) M.-V. (i.) L.p.	(b) P.p. (i.) ant. (ii.) post. (c) M.-V. (i.) L.p.	"22" (Owen). Trapezius.  Levator scap.
	(c) M.-V. derivs. (i.) L.p. (ii.) C.a.c. (iii.) C.-br. (iv.) C.-hy. (v.) C.-hm. (vi.) C.-m.	(ii.) C.-br. (iii.) C.-hy. (iv.) C.-m.	(ii.) C.-br. (iii.) C.-hy. (iv.) C.-m.	(ii.) C.-br. (iii.) C.-hy.	(ii.) C.-br. (iii.) C.-hy.	Sternohyoid.
FISH MUSCLES.	(a) Add. (i.) sup. (ii.) prof.	(a) Add. (i.) sup. (ii.) prof.	(a) Add. (i.) sup. (ii.) prof.	(a) Add. (i.) sup. (ii.) prof.	(a) Add. (i.) sup. (ii.) prof.	
	(b) Abd. (i.) sup. (ii.) prof.	(b) Abd. (i.) sup. (ii.) prof.	(b) Abd. (i.) sup. (ii.) prof.	(b) Abd. (i.) sup. (ii.) prof.	(b) Abd. (i.) sup. (ii.) prof.	





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TARSUS SPECTRUM.

9. Notes on the living Tarsier (*Tarsius spectrum*).

By W. E. LE GROS CLARK, F.R.C.S. Eng., F.Z.S.

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(Plate I.\* ; Text-figure 1.)

The work of comparative anatomists has of late drawn particular attention to the Tarsier as representing an animal which shows considerable affinities on the one hand to lemurs and insectivores, and on the other to the anthropoidea. While the discussion which took place at the Zoological Society four years ago served to show that the views of zoologists regarding the precise systematic position of the Tarsier were not wholly in accord, it was agreed that, to whatever position it should be allocated in the order of Primates, the animal showed many features which allied it to the monkeys and even higher primates, and the general conclusion seems to be that it should be placed in a special suborder which occupies a position more or less intermediate between the lemuroidea and the anthropoidea. In connection with the interesting anatomical features of the Tarsier, it will perhaps be instructive to record observations which I was able to make on the living animal during the three years of my stay in Sarawak.

I must admit that I have never had the good fortune to see a Tarsier in the wild state. Many times I have wandered into the parts of the jungle where I knew the animal had been obtained, but I was never rewarded for my trouble by seeing one myself there. The specimens which I kept in captivity were brought to me by Dyaks, who usually came across them while felling trees in the jungle during the day-time.

The animal is readily caught, for when disturbed in the day-time, it makes no attempt at rapid escape, but usually merely turns its head towards the intruder with widely open eyes and slightly gaping mouth, often so adjusting its position that the branch to which it is clinging is kept between it and the threatened danger.

*Habitat.*

All the specimens of Tarsier which I have collected have been obtained in Sarawak, and with one exception, all were captured in the neighbourhood of Kuching. They were all found in jungle of the secondary type, or in recently cleared primary jungle. The animal would appear to inhabit comparatively low-lying country,

\* For explanation of the Plate see page 223.

the greatest altitude at which one of my specimens was found being between two and three hundred feet above sea-level, at Bukit Siul, close to Kuching.

Enquiries among natives failed to elicit any information regarding the animal's life in the jungle, and there is no evidence that it builds a nest or lives in holes in trees as has occasionally been asserted.

The Tarsier is usually found in single pairs except at the end of the breeding season, when the female and young are found alone.

### *Habits.*

When at rest the Tarsier clings to a vertical branch, the palms of the hands and soles of the feet closely applied to the surface of the bark. While the hallux is always very distinctly opposed to the other digits in grasping the branch, this is not the case with the pollex. The animal is largely supported in this vertical position by its tail, the ventral roughened surface of which is pressed against the branch below. If the tail is carefully lifted away from contact with the branch, the animal is deprived of some of its support and the body tends to sink down. If the tail now be let go, it springs back sharply to its former position by muscular action. The tail is not in any way prehensile in the true sense of the word.

When the animal sleeps in this position, the head is allowed to sink forwards between the two upper limbs so that the tip of the head comes in contact with the branch to which it is clinging. If disturbed, the Tarsier usually shifts its position (as described above), in order, apparently, to protect itself behind the branch to which it clings, and assumes an attitude of alertness ready to spring to another branch. Its ears are turned towards the source of any noise, and it opens its mouth partly, showing its sharp teeth. This latter action was described by Cuming \*, and has been noted by Pocock as resembling the monkey's habit of baring its teeth when approached, and quite unlike the attitude adopted by lemurs under corresponding conditions.

If disturbed further, the Tarsier will either leap to another branch and once more turn to face its pursuer or, more often, it will stay its ground and show fight. In the latter case, if a finger is brought up close to it, the animal will usually make a dash at it, seize it between its two hands and, with tightly closed eyes, will endeavour to bite. One male Tarsier which I had was even bolder, and would spring at the face of the intruder and blindly try to bite whatever portion offered itself.

The accuracy with which the Tarsier leaps from branch to branch in the day-time is astonishing, for, judging by the clumsy way in which it seizes food offered to it, it would appear to be unable to see very clearly in the sunlight.

\* Cuming, Proc. Zool. Soc. 1838.

The animal is seen at one moment clinging to a branch, and the next moment is clinging to another branch a yard away in precisely the same position, the observer catching a glimpse of the animal flying through the air with tail streaming behind in the very brief interval.

On a flat surface the Tarsier progresses in a fashion very similar to that of a frog, by a series of leaps, landing again in a sprawling attitude. Only very occasionally does it take a few steps forwards in an awkward manner.

With regard to food, I have only been able to persuade the Tarsier to take grasshoppers and drink milk or water. On being offered a grasshopper, the animal stares at it for a moment or so, drawing itself up and adjusting its position so as best to spring on the insect. This it does with both its forelimbs, seizing hold with its long fingers and raking in the morsel to its mouth, which is protruded forwards as far as possible to assist in the capture.

The animal screws up its eyes very tightly when seizing its prey, and in the day-time it appears to find great difficulty in accurately locating the grasshopper, for it will often seize and bite the fingers or forceps which hold the insect. The latter is crammed into the mouth and scrunched up, protruding portions being helped in by one of the hands.

The careless and blundering way in which the Tarsier seizes its prey is in marked contrast to that of the slow Loris. This animal very carefully surveys the insect from all sides, swaying to and fro in a curiously serpentine fashion, and then, in a flash, seizing it neatly with its two hands. The Tarsier takes milk by lapping with the tongue.

It is interesting to note the way in which the animal performs its toilet. This is done by licking the fur after the manner of a cat, and when the turn of the hind limbs comes, these are supported in a stretched-out position by being grasped with the hand of the same side.

The hind limb is used for scratching purposes, the digits of the pes being flexed on to the sole in such a way that only the two claws on the second and third digits are left protruding.

With regard to noises, the Tarsier is ordinarily silent on every occasion observed. The young, however, emit a shrill, almost inaudible squeak at short intervals if left alone. I once heard a similar sound given by an adult female. She had, however, been injured in the process of capture, and no doubt was suffering pain.

### *The Young.*

The Tarsier gives birth to a single young at a time. The statement has been attributed to Hose in some books that the Tarsier carries its young in its mouth as a cat carries her kitten. I have kept under observation seven female Tarsiers and young, and have never been able to confirm this. On enquiring from Dr. Hose, this author, in a private communication, tells me that he

has been quoted erroneously, and that he has never made any statement of this kind. On the contrary, he says that he has never seen the young carried in any other manner but the one which I describe, although some natives have told him that they are sometimes carried by the teeth. The statement in literature probably emanated from Cuming, who stated in 1838 that he watched a female endeavouring to escape from its cage, holding her baby in her teeth. I can merely state that I have never seen this occur, nor have I been able to persuade the natives who brought me specimens to give evidence to support this statement. The young always cling on to the fur of the mother's abdominal wall, grasping with both hands and feet, and are not in any way actively held by the mother. In this way the little animal is very often wholly concealed from view when the mother is in the resting position, clinging to a branch.

On one occasion when the mother was sleeping in the position already described, her baby was found sitting on the top of its mother's bent head, clinging on to the branch above with its hands.

At birth, the Tarsier has reached a comparatively advanced stage of development. The eyes are open, and though its movements are uncertain, the animal can cling to a vertical branch, and scramble about the branches in a hesitating way. When disturbed it assumes an appearance of alertness, turning its head towards the source of disturbance. During the first month of its life it is not able to leap from branch to branch, though it can progress along the ground by a series of short jumps. At the end of three weeks the young Tarsier will take a grasshopper offered to it, but it is evident this diet does not agree with the animal at this early age.

The breeding season of *Tarsius*—in Sarawak at least—appears to correspond to the season of the north-east monsoon, i.e. from October to March, and in this it agrees with other mammals on which I have made observations in Borneo.

The following is a list of the embryos and young which I have been able to obtain, with the dates of capture.

1. Embryo of 13-14 somites.....	December, 1920.
2. Embryos,, 25 mm.....	Oct. 30th, 1921.
3. " " 33 mm.....	Oct. 18th, 1921.
4. Early embryo (not yet sectioned) .....	Dec. 8th, 1921.
5. Fœtus (prematurely born) ..	Jan. 1st, 1923.
6. New-born young .....	Jan. 6th, 1923.
7. Recently-born young (maternal uterus not yet involuted) .....	Feb. 22nd, 1923.
8. Recently born young .....	Feb. 26th, 1923.

From these data it will be seen that impregnation may take place as early as October and as late as December, while the young are, as a rule, born in the early months of the year.

*General description of Tarsius.*

Elliot, in his 'Review of the Primates,' describes no fewer than seven distinct species of this animal, and, judging from the paucity of his material, it is to be very much doubted whether he is justified in making these specific distinctions. His description of *Tarsius borneanus* (Elliot) is admittedly based on the examination of an immature specimen, and for this reason, and because his description is not fully corroborated by an examination of a larger number of specimens, I find it necessary to give here a new description of the Bornean variety.

*TARSIVS SPECTRUM (v. BORNEANUS).*

General colour a brownish-red with underlying mouse-grey. The eyelids, cheeks, submental region, rump, and lateral aspect of thighs in the adult, and more especially in the female sex, are a rust-red. Flexor surface of thighs and ventral aspect of base of tail whitish-yellow. Ventral surface of thorax and abdomen covered with grey hair tipped with whitish. Black patch over anterior part of maxillæ at the side of the nose. Throat pale yellow. Ears dark reddish-brown, naked. Tarsi and haired portion of tail light brownish yellow, the caudal hairs being tipped with darker reddish brown. Along the inner surfaces of the thighs is a relatively bare area, very sparsely covered with hair. Dorsum of pes and manus dark brown, palmar and plantar surfaces unpigmented. Iris yellowish brown. The rufous coloration on the face, rump, and lateral surfaces of the thighs is very distinctly more marked in the adult females than in the adult males of my collection, and there is little doubt that this may be regarded as a definite sexual feature.

For the young animal the above description holds good except that the rufous markings are not so well developed. The iris at birth has a definite blue tint, which rapidly fades as the animal grows, passing through a light greenish-brown phase to reach the adult coloration.

In the new-born young the hairs on the tail are distributed more or less evenly from base to tip, and it is only when the animal reaches a stage of development corresponding to a weight of about 30 grams that the terminal caudal tuft of hairs is well demarcated off from the relatively bare proximal portion of the tail.

Another interesting feature is that in living individuals recently born, the skin of the tail is marked off in alternating light and dark bands, which though faint, are quite distinct.

There is little to add to the account by Pocock\* of the external characters of the Tarsier. This author denies the presence of

\* Pocock. "On the External Characters of the Lemurs and Tarsiers," Proc. Zool. Soc. vol. i. 1918.

genal and carpal vibrissæ in the animal. I have, however, found genal vibrissæ in all but two of my specimens, and they are situated in a position similar to those of *Galago* and *Hemigalago*.

I have not been able to distinguish carpal vibrissæ in the adult animal, but there is a very distinct carpal vibrissa in the foetal specimen (prematurely born) which I obtained. It is situated on a rounded eminence immediately proximal to the hypothenar pad (text-fig. 1). It is clear, therefore, that *Tarsius*

Text-figure 1.



Fore limb of fetal *Tarsier*, illustrating the presence of a carpal vibrissa.

forms no exception in this respect to the majority of arboreal mammals.

The hair tracts of *Tarsius* (as determined in the foetal specimen) correspond accurately with the description given by Schwalbe.

With regard to the external proportions of the adult *Tarsier*, the following list represents the average of measurements of ten adult specimens. No sexual difference is noticeable in these proportions.

	Av.	Max.	Min.
Body length (D.C.L.) .....	154 *	162	149
Tail .....	216	224	208
Caudal tuft .....	65	75	55
Head length .....	42	44	40
Head breadth .....	33	34	32
Brachium .....	29	30	27
Forearm .....	40	43	39
Manus .....	45	48	43
Thigh .....	65	70	55
Leg .....	64	67	58
Pes.....	68	71	64
Weight .....	114	142.5	92.3

Below are appended the weights and proportions of three young *Tarsiers*. The first specimen (16  $\alpha$ ) was obtained the day after birth (the animal having been born on the evening of capture). In the case of the second specimen (No. 16), the maternal uterus was as yet incompletely involuted, so that the young animal may

\* Length measurements are in millimetres, and weights in grams.

be assumed to have been but a few days old. The age of the third specimen (No. 18) is not accurately known, but since its proportions correspond very closely to the two former, it was almost certainly comparatively newly born.

	16 a*.	16*.	18.
Length of body (D. C. L.) .....	—	—	100
"    "    tail .....	93	89	86
Head length .....	—	—	31
Head breadth .....	—	—	22
Brachium .....	14	14	14
Forearm .....	20·5	20	20
Manus .....	24	24	26
Thigh .....	30	31·5	30
Leg .....	27	28	29
Pes .....	36	38	38
Weight ... ..	23·1	—	24

*Notes on the blood test.*

In view of the claims made by some authorities for the very close affinities of *Tarsius* with man, it will be of interest to record the result of the precipitin test on the fresh blood of the animal. With the assistance of Dr. O'Driscoll, Pathologist to the Sarawak Government, I carried out this test, using serum sensitized to human blood, and using as controls the blood of Man, *Simia*, *Hylobates*, *Macacus*, *Nycticebus*, *Sciurus*, and *Felis*. Positive results were obtained with the first three. The blood of *Tarsius*, with that of the other animals above mentioned, was completely negative.

In conclusion, I should like to express my gratitude to His Highness the Rajah of Sarawak in whose service I had the honour of working and who granted me permission to collect and export the specimens which I obtained in Borneo.

\* The measurements of these specimens are incomplete owing to the fact that the animals were decapitated to secure their skulls before the measurements were taken.

## EXPLANATION OF THE PLATE.

### PLATE I.

Fig. 1. Female Tarsier with young.  
2. Young Tarsier.

Fig. 3. Adult male Tarsier.  
4. Adult male Tarsier.





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1. RHACOPHORUS CHASENI. 2. R. NOTATER. 3. R. CALCANEUS.



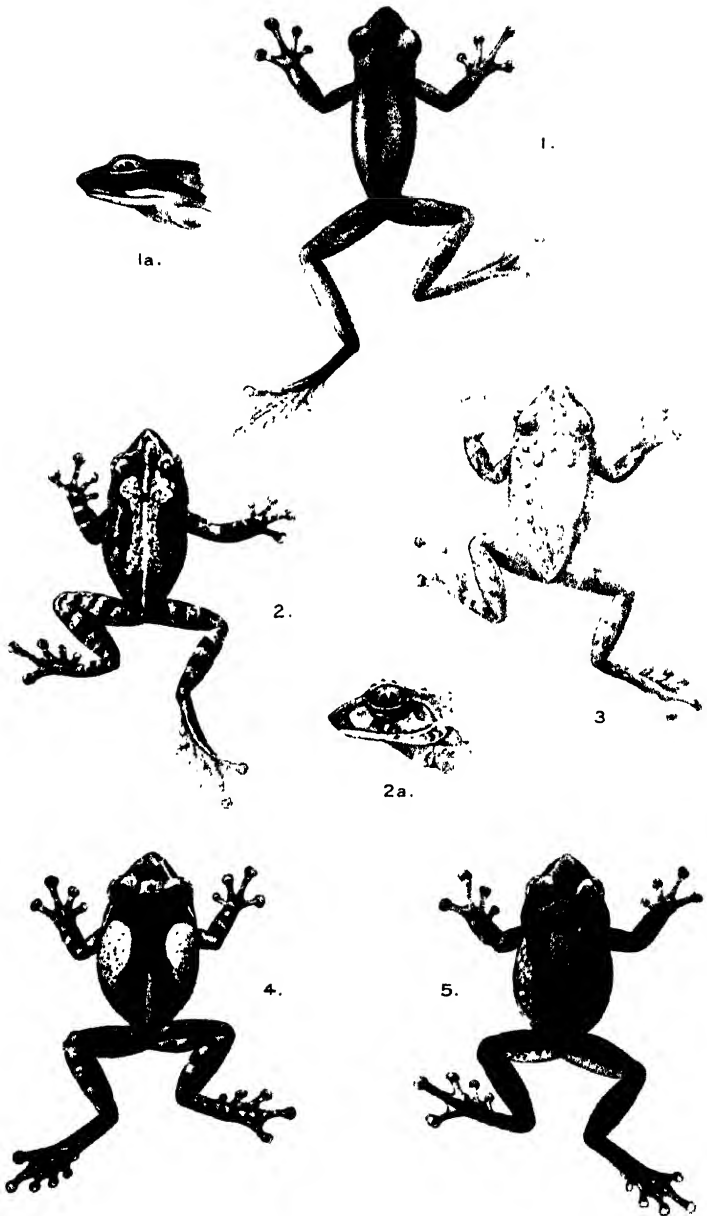


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1. RHACOPHORUS ANNAMENSIS. 2. PHILAUTUS LAEVIS.





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1. *PHILAUTUS PALPEBRALIS*. 2, 3, 4, 5, *P. GRYLLUS*.

10. New Tree-Frogs from Indo-China and the Malay Peninsula. By MALCOLM A. SMITH, M.R.C.S., L.R.C.P., F.Z.S.

(Plates I.-III.\* and Text-figure 1.)

[Received August 28, 1923: Read February 5, 1924.]

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The Tree-Frogs acquired by me through various expeditions during the last few years have for one reason or another been set aside undetermined. I have recently examined this accumulation of material, and the following species in the collection appear to be new to Science.

The types of the new species here described have been presented to the British Museum of Natural History.

Other species which are worthy of record are the following :—

*Rhacophorus colletti* Boulenger, 1890.

Two specimens collected by Mr. C. J. Aagnard at Bangnara, Patani, Peninsular Siam. This frog has not previously been recorded from the Asiatic mainland.

*Rhacophorus verrucosus* Boulenger, 1893.

Many examples from the Langbian Plateau, S. Annam. To this species also I refer the *Rh. curirostris* recorded by Sclater from Tenasserim (P. Z. S. 1896, p. 346). Dr. Annandale has kindly sent me the specimen for examination.

*Philautus vittatus* (Boulenger) 1887.

A common frog at Ta Rua in Central Siam and Nong Khor, Sriracha, S.E. Siam, both localities being practically at sea-level. I have specimens also from Cap St. Jacques, Cochin China.

\* For explanation of the Plates see page 234.

*Chirixalus doriae* Boulenger 1893.

Also common at Nong Khor, where it lives in company with the preceding species. I have a specimen also from Ban Khen, Me Wang forest, N. Siam.

**RHACOPHORUS CHASENI, sp. n.**

Type, adult female with ripe ova, author's number 5972, collected by the Teku River, alt. 1500 m., Gunong Tahan, Malay Peninsula, by Mr. F. N. Chasen, of Raffles Museum, Singapore, in December 1921. I have much pleasure in naming it after him.

Description of the type. — Vomerine teeth in two slightly oblique groups touching the anterior inner borders of the choana; tongue deeply indented, without papilla. Head longer than broad, much depressed, triangular in shape; skin over the cranial region not adherent to the bone; snout acutely pointed, projecting beyond the nostrils in a pronounced tip, much longer than the orbit; canthus rostralis distinct; loreal region very oblique, concave; nostril considerably nearer the tip of the snout than the eye; interorbital space nearly twice as broad as the upper eyelid; tympanum distinct, three-fifths the diameter of the eye, its distance from the eye half its own diameter, clearly visible from above owing to the unusual slope of the temporal region.

Outer two fingers nearly half webbed, inner fingers slightly less; discs of the fingers as broad as long, two-thirds the size of the tympanum; toes fully webbed, their discs not as large as those of the fingers; subarticular tubercles well developed; a prominent inner metatarsal tubercle one-third the length of the inner toe, no outer tubercle. Hindlimb slender, the tibia six times as long as broad, the tibiotarsal articulation reaching nearly to the nostril.

Skin smooth above, strongly granular on the belly and below the thighs, throat smooth; a fold from the eye to the shoulder; a feebly denticulate dermal fold from the elbow along the outer side of the forearm and hand, another along the outer side of the foot terminating at the tarso-metatarsal joint in a pointed flap; a strong fold below the vent interrupted in the middle, and a denticulate fringe along the ramus of the lower jaw.

Greyish above, speckled with darker; below greyish white. Inner fingers and toes paler than the outer; interdigital membranes dark grey.

A second specimen collected by the Federated Malay States Museum in the same locality does not differ much from the above.

*Rhacophorus chaseni* is closely related to *Rh. appendiculatus* Günther, from the Philippine Islands. It differs in the narrower head and more oblique temporal region, in the broader web to the fingers and more slender limbs, and in the stronger dermal

fringes along the outer aspects of the limbs and lower jaw. To this species also I refer a specimen in the British Museum from Balingeen, Sarawak, and three more in the Raffles Museum, Singapore, from the Baram River, N. Borneo, all of which had been identified as *Rh. appendiculatus*.

Adult examples of *Rh. appendiculatus* (51 mm. from snout to vent) from South Mindanao, recently sent me by Mr. Edward H. Taylor, have enabled me to compare the two species. Gunther's figure (Cat. Batr. Sal. Brit. Mus. 1882, pl. viii. fig. 4) drawn from an immature specimen gives but a poor impression of the pronounced "nose" which the adult develops. It is nearly as large as that of *Rh. chaseni*.

Measurements of *Rh. chaseni* in mm.

No.	5972	6006	6626
Sex	♀	♀	♀
Snout to vent	50	46	50
Length of head	16	16	16
Breadth of head	17	17	17
Snout	8.5	7	8.5
Eye	5	5	5.5
Tympanum	3.5	2.5	3
Forelimb	30	27	28
Hand	13	12	13.5
Hindlimb	77	70	74
Tibia	27	26	25
Foot	20	19	21
Locality	Gunong Tahan. Gunong Tahan. Baram River.		

*RHACOPHORUS NOTATER*, sp. n.

Type, author's number 2797, collected at Daban, alt. 200 m., Phan Rang province, S. Annam, in April 1918.

Description.—Head as long as broad, snout rounded; nostril nearer the tip of the snout than the eye; loreal region nearly vertical; interorbital space as broad as the upper eyelid; tympanum indistinct, about half the diameter of the eye, and close to it.

Outer two fingers two-thirds webbed, inner fingers less; discs of the fingers about as large as tympanum. Toes nearly fully webbed, their discs smaller than those of the fingers; subarticular tubercles well developed; a small oval, inner metatarsal tubercle, no outer; outer metatarsals completely separated. The tibio-tarsal articulation reaches the tip of the snout.

Skin of the back quite smooth, throat smooth, belly and below the thighs coarsely granular. A feebly developed dermal ridge along the outer side of the forearm and foot. A fold from the eye to the shoulder.

Pale grey above with large irregular black blotches; limbs with dark bars. Below white.

Remarks.—This frog was taken as a tadpole leaving the water



and survived one week, during which time its colour changed completely. Its characters are therefore not yet fully developed, but the combination of webbed fingers, smooth skin, and unusual coloration are sufficient to distinguish it. A second specimen has the dermal ridge along the outer side of the limbs more strongly developed.

*RHACOPHORUS CALCANEUS*, sp. n.

Type, male, author's number 2409, collected at Langbian Peaks, alt. 2000 m., S. Annam, in April 1918.

Description.—Vomerine teeth in feebly oblique series, commencing opposite the anterior inner borders of the choanæ but not touching them. Head a little broader than long, moderately depressed; snout obtusely pointed, projecting feebly beyond the mouth, longer than the eye; nostril nearer the tip of the snout than the eye; canthus rostralis distinct; loreal region oblique, feebly concave; interorbital space broader than upper eyelid; tympanum distinct, three-fifths the diameter of the eye, its distance from the eye half its own diameter.

Outer two fingers three-fourths webbed, inner two one-fourths webbed; discs of the fingers broader than long, that of the third being larger than the tympanum. Toes nearly fully webbed, their discs smaller than those of the fingers; subarticular tubercles well developed; a small oval, inner metatarsal tubercle, no outer; outer metatarsals nearly completely separated. Tibia  $4\frac{1}{2}$  times as long as broad; the tibiotarsal articulation reaches the middle of the eye.

Skin above quite smooth; belly and under surface of thighs coarsely granular; a strong fold from the eye to the shoulder; heel with a well-marked pointed terminal tubercle; a rather broad feebly distinct ridge along the outer side of the forearm and another along the outer side of the foot; a series of indistinct tubercles below the vent.

Olive above (pale green in life when first caught), with numerous small punctate dots of pale yellow, chiefly on the back. A yellow line extending from the tip of the nose along the canthus rostralis and along the outer edges of the upper and lower eyelids. Upper lip, whole of lower parts and inner three fingers and four toes pale yellow; outer fingers and toes yellow and olive; interdigital membranes of outer fingers and toes with dark spots; a round spot in the axilla and another—on one side only—in the groin.

Nearest to *Ih. bimaculatus* Blgr., from the Malay Peninsula and Siam, from which it differs in the position of the vomerine teeth, in the feebler dermal ridge along the outer sides of the arm and leg and absence of skin-flap above the vent, in having a tubercle at the heel instead of a flap, and in the shorter interdigital membrane.

Type unique.

## Measurements in mm.

Snout to vent . . . . .	38	Forelimb . . . . .	24
Length of head . . . . .	13	Hand . . . . .	12
Breadth of head . . . . .	14.5	Hindlimb . . . . .	55
Snout . . . . .	6.5	Tibia . . . . .	19
Eye . . . . .	5	Foot . . . . .	16
Tympanum . . . . .	2.5		

*RHACOPHORUS ANNAMENSIS*, sp. n.

Type, male, unique, author's number 2450, collected at Daban, alt. 200 m., Phan Rang province, S. Annam, in April 1918.

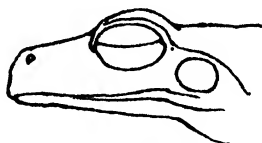
Description.—Vomerine teeth in almost straight transverse series commencing from the anterior inner ends of the choanæ. Head slightly broader than long, much depressed; snout rounded, feebly projecting beyond the mouth, longer than the eye; nostril a little nearer the tip of the snout than the eye; canthus rostralis fairly distinct; loreal region oblique, concave; interorbital space broader than upper eyelid; tympanum distinct, half the diameter of the eye, distant from the eye less than half its own diameter.

Fingers broadly webbed, the membrane between the outer three fingers reaching the discs; discs broader than long, that of the third larger than the tympanum. Toes fully webbed, their

Text-figure 1.

*Rh. annamensis.*

× 1½.

*Rh. pardalis.*

× 1½.

discs considerably smaller than those of the fingers; subarticular tubercles well developed; a small oval, inner metatarsal tubercle one-third the length of the inner toe, no outer tubercle; outer metatarsals separated to the base. Tibia  $4\frac{1}{2}$  times as long as broad; the tibiotarsal articulation reaching the front of the eye.

Skin above smooth with sparsely scattered flat tubercles; belly and under surface of thighs coarsely granular; a fold from the eye to the shoulder; a well-marked fringe along the outer side of the forearm and hand, another less prominent along the outer side of the foot; a tarsal fold with a small tubercle which is not continuous with the dermal fringe; a series of tubercles below the vent.

Brown above with dark markings, the most conspicuous being

an indistinct **X** upon the nape and dark cross-bars upon the limbs; sides mottled with brown and yellow; yellow beneath (white in life), the throat with a few brown spots. Interdigital membranes brown above, yellowish below.

Remarks.—*Rh. annamensis* is closely related to *Rh. pardalis* Günth., from Borneo and the Philippines. I have compared it with a specimen from Borneo and find it differs in the following particulars:—

In *pardalis* the snout descends almost vertically in front of the nostrils; the space between them above is concave and the canthus rostralis is strongly marked.

In *annamensis* the snout is prolonged and slopes gradually beyond the nostrils; the space between them is flat and the canthus rostralis is not strongly marked.

*pardalis* has a pronounced rudimentary pollex, *annamensis* has not; *pardalis* has a strong dermal flap at the heel which is continuous with the fringe along the outer side of the foot. In *annamensis* there is a small tubercle only which is not continuous with the fringe along the foot.

Measurements of *Rh. annamensis* in mm.

Snout to vent	61	Forelimb	34
Length of head	19	Hand	17
Breadth of head	20	Hindlimb	92
Snout	9	Tibia	31
Eye	7	Foot	26
Tympanum	3.5		

*PHILAUTUS LAEVIS*, sp. n.

Type, male, author's number 2439, collected at Sui Kat, alt. 1000 m., Langbian Plateau, S. Annam, in March 1918.

Description. —General configuration uniform. (Choanae small, rounded, partly hidden by the edge of the jaw. Head as long as broad, much depressed; snout obtusely pointed, longer than the eye, slightly projecting beyond the mouth; canthus rostralis fairly distinct; loreal region oblique, scarcely concave; nostril very near the tip of the snout, interorbital region broader than upper eyelid; tympanum distinct, half the diameter of the eye, its distance from it equal to its own diameter.

Fingers quite free, first half the length of the third, fourth shorter than the second, disc of the third smaller than the tympanum; toes one-third webbed, their discs about as large as those of the fingers; subarticular tubercles moderate; palmar and plantar surfaces of the hands and feet smooth; a small oval, inner metatarsal tubercle, no outer; the tibiotarsal articulation reaches nearly to the nostril.

Skin of the upper parts, throat, and chest quite smooth, abdomen and thighs feebly granular.

Colour in life: Rich buff above with ill-defined darker longi-

tudinal streaks; a pale yellow band on either side of the back from the eye to the hip; sides of the head and body darkish brown; tympanum reddish. Below pure white.

This small frog is related to *P. vittatus* Blgr. from Burma, Siam, and Cochin China. It is easily distinguished from it by the distinct tympanum, shorter fourth finger, shorter web to the toes, and coloration.

Type unique.

#### Measurements in mm.

Snout to vent . . . .	26	Hindlimb . . . .	39
Length of head . . . .	8.5	Tibia . . . . .	13
Eye . . . . .	3	Foot.. . . .	10
Forelimb . . . . .	13		
Hand . . . . .	6		

#### *PHILAUTUS GRILLUS*, sp. n.

Type, adult male, author's number 4962, collected on Langbian Peaks, alt. 2000 m., Langbian Plateau, S. Annam, in March 1918.

Description of type.—Tongue deeply nicked behind, choanæ small, rounded, not hidden by the edge of the jaw. Head broader than long; snout pointed, longer than the orbit; canthus rostralis fairly distinct; loreal region oblique, slightly concave; nostril a little nearer the tip of the snout than the eye; inter-orbital region slightly broader than upper eyelid; tympanum indistinct, two-fifths the diameter of the eye.

Fingers free except for a rudiment of a web between the two outer; disc of the third as large as the tympanum. Toes a little more than half webbed, their discs not quite as large as those of the fingers; subarticular tubercles single; palmar and plantar surfaces of hands and feet with numerous granules of uneven size; a small inner metatarsal tubercle; outer metatarsals separated for about two-thirds of their length; the tibiotarsal articulation reaches the anterior border of the eye.

Upper parts smooth except for small tubercles on the upper eyelid and head; throat finely granular, belly and lower surfaces of thighs coarsely granular; heel with a small pointed appendage; a series of tubercles along the outer side of the forearm and foot; a fold above the tympanum.

Above yellowish grey, uniform except for a few indistinct darker markings, an X-shaped mark being just indicated upon the back. Yellowish white beneath.

Variation.—Fifty-one specimens examined show the following variations from the above. The tympanum in some adults is not visible at all; the snout may be pointed as in the type, owing to the presence of a dermal tip, or lacking this is subacuminate in outline; the nostril may be equidistant between the tip of the snout and the eye, the interorbital region no broader than the

upper eyelid; the toes may be two-thirds webbed, the membrane reaching the disc of the fifth, but not that of the third, and leaving two phalanges of the fourth free; some examples have pointed tubercles upon the back. The male has a large subgular vocal sac.

Coloration extremely variable. In life various shades of light or dark brown, green, yellow, or grey were met with. Many had a bright green patch on the snout, and patches of similar colour on the knees and round the vent. Some are uniform in coloration, others have a )(-shaped mark upon the back enclosing a dark patch and the remaining parts uniform or thickly speckled. A few examples are spotted with brown on the underparts.

Remarks.—*P. gryllus* is most nearly related to *P. aurifasciatus* (Schleg.) and *P. petersi* (Blgr.), from both of which it differs in the shorter leg, more fully webbed toes, and in the fringe of tubercles along the outer sides of the limbs.

This small Tree-Frog was common round our camp at the Langbian Peaks; it was also plentiful at Dalat, Camly, and Arbrey Broyé, localities some 400 metres lower on the plateau. One example was taken at Sui Kat, 1500 metres altitude. It frequented small bushes, chirruping at night much like a cricket, by which cry it could be tracked down with a lantern and caught. Thus it is that in spite of the large series obtained all of them are males.

#### Measurements of specimens in mm.

No.	.....	4962	2389	2396
Snout to vent	.....	25	27	27
Breadth of head	.....	10	11	10
Length of head	.....	8	9.5	9
Eye	.....	3	3	3.5
Snout	.....	4.5	4.5	4
Hand	.....	7.5	8.5	8
Leg	.....	37	39	37
Tibia	.....	12	13	13
Foot	.....	11	11.5	11

The tadpole which I associate with this species was obtained at Dalat, and was common in a small stream there.

Description.—Head and body about one-third longer than broad, not markedly depressed. Nostrils a little wider apart than the interocular breadth, equidistant between the eye and the tip of the snout, which is rounded. Spiraculum sinistral, pointing backwards and upwards, nearer the eye than the vent, which is dextral. Mouth subterminal; a fringe of papillæ at the sides and below; beak narrowly edged with black; upper lip with five or six rows of teeth, the first two long and continuous, the lower three or four broadly interrupted; lower lip with four long rows, the uppermost of which is narrowly interrupted. Tail  $3\frac{1}{2}$  times as long as high, obtusely pointed, crests moderate,

subequal. Colour brownish, speckled above and on the sides with darker.

Measurements of a well-grown specimen with budding hind-limbs:—Length of head and body 14 mm., breadth of body 10 mm.; length of tail 29 mm., greatest height of tail 8 mm.

*PHILAUTUS PALPEBRALIS*, sp. n.

Type, female, author's number 2589, collected on Langbian Peaks, alt. 2000 m., S. Annam, in April 1918.

Description.—Tongue deeply notched behind, no papilla; choanæ small, rounded, partly hidden by the overhanging edge of the jaw. Head as long as broad, moderately depressed; snout obtusely pointed, feebly projecting beyond the mouth, a little longer than the eye; nostril nearer the tip of the snout than the eye: canthus rostralis distinct; loreal region nearly vertical, concave; interorbital space as broad as the upper eyelid; tympanum almost hidden, two-fifths the diameter of the eye, its distance from the eye equal to its own diameter.

First two fingers partially opposed to the others; a rudiment of a web between the outer two; discs as long as broad, that of the third as large as the tympanum. Toes half webbed, their discs smaller than those of the fingers. Subarticular tubercles well developed, palmar and plantar surfaces of hands and feet with numerous granules; inner metatarsal tubercle one-third the length of the inner toe; no outer tubercle; outer metatarsals separated for half their distance; the tibiotarsal articulation reaches the eye.

Skin quite smooth except on the belly and lower aspects of the thighs where it is coarsely granular; a feeble fold above the tympanum.

Reddish brown above, uniform, pale yellowish below. A yellow streak from below the eye to the shoulder; nictitating membrane thickly speckled with brown. A green spot on the occiput in life.

*Philautus palpebralis* appears to be most nearly related to *Chirixalus doriae* Blgr., from Burma to Siam. It differs in the hidden tympanum and the shorter web to the toes, in having the two inner fingers less completely opposed to the outer, and in many other small characters which are evident on comparison.

Type unique.

Measurements in mm.

Snout to vent .. .. .	30	Hindlimb .. . . .	45
Breadth of head .. . . .	9	Tibia .. . . .	15
Eye .. . . .	3	Foot .. . . .	13
Forelimb .. . . .	19		
Hand .. . . .	8		

## EXPLANATION OF THE PLATES.

## PLATE I.

1. *Rhacophorus chaseni*, sp. n.
- 1 a.       "               "       "
2. *Rhacophorus notater*, sp. n.
3.       "       *calcanus*, sp. n.
- 3 a.       "               "       "

## PLATE II.

1. *Rhacophorus annamensis*, sp. n.
2. *Philautus laevis*, sp. n.
- 2 a.       "               "       "

## PLATE III.

1. *Philautus palpebralis*, sp. n.
2.       "       *gryllus*, sp. n.
- 2 a.       "       "       "
3.       "       "       "
4.       "       "       "
5.       "       "       "







1.

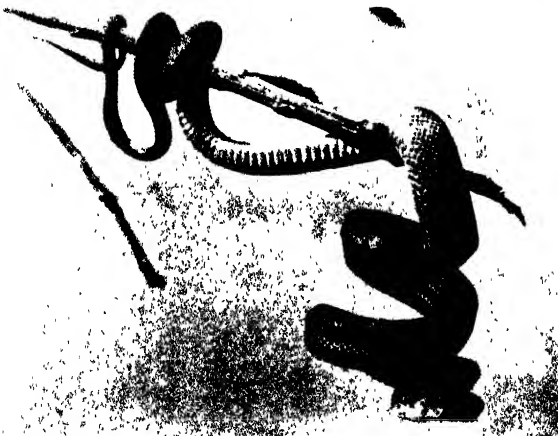


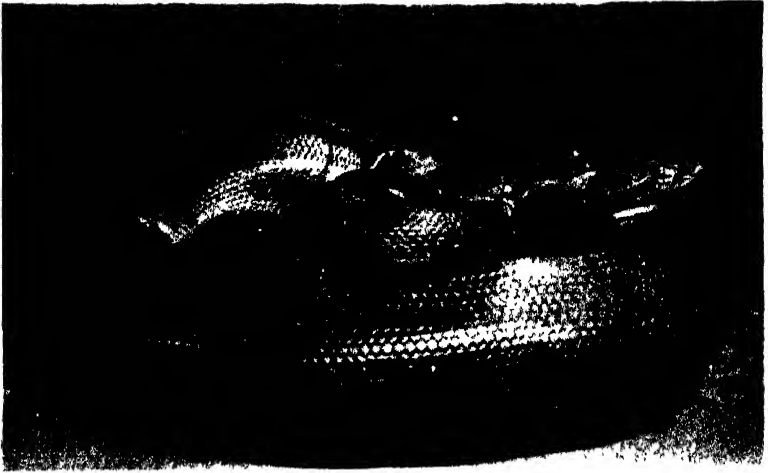
Photo F. W. Ulrich

John Baie Sons & Danielsson Ltd

2.

TRINIDAD SNAKES.





1



Photo F. W. Birch

Photo F. W. Birch & Denzilson L. H.

2

TRINIDAD SNAKES





1.



Photo F. W. Ulrich

John Bale Sons & Danielsson Ltd

2.

TRINIDAD SNAKES



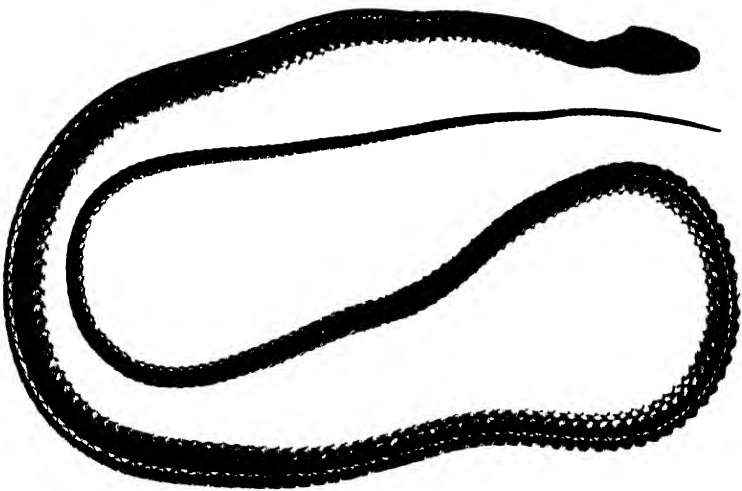
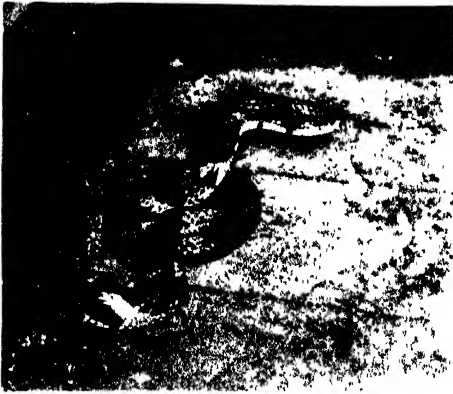


Photo F. W. Ulrich.

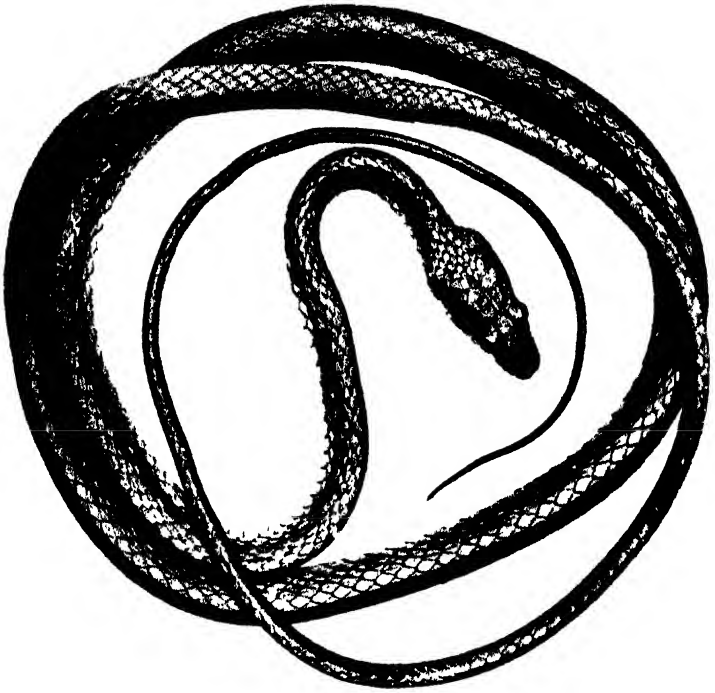
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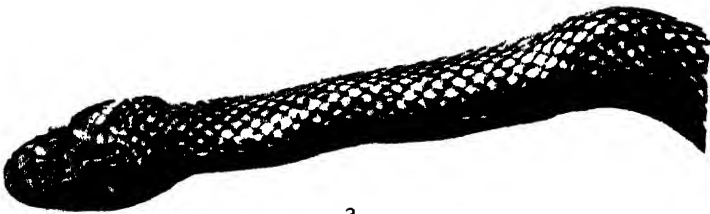
TRINIDAD SNAKES







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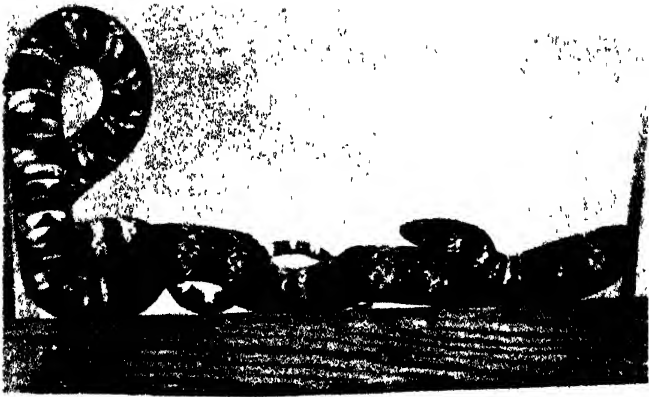
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Photo F. W. Ulrich

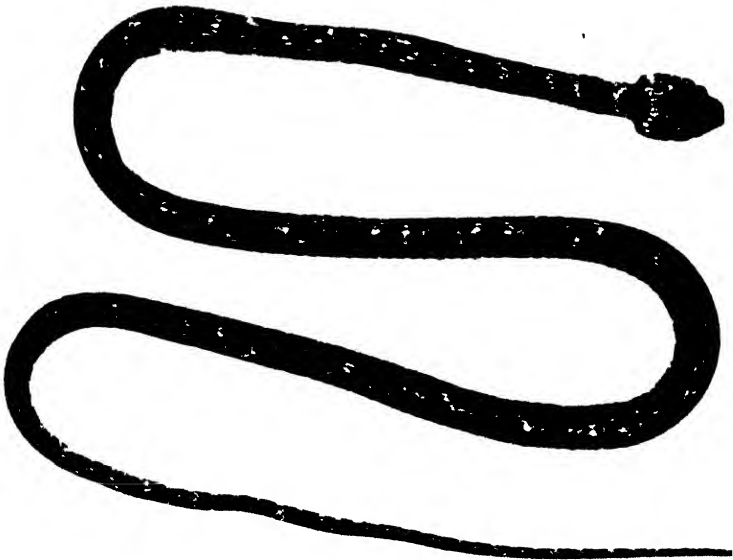
John Bale Jones & Danielsson Ltd

TRINIDAD SNAKES<sup>4</sup>





1



2.

Photo F. W. Ulrich

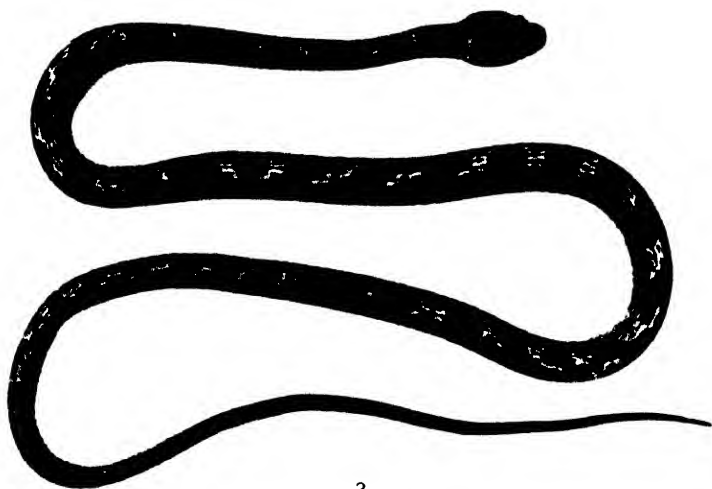
John Bates Smith & Danielsson

TRINIDAD SNAKES.





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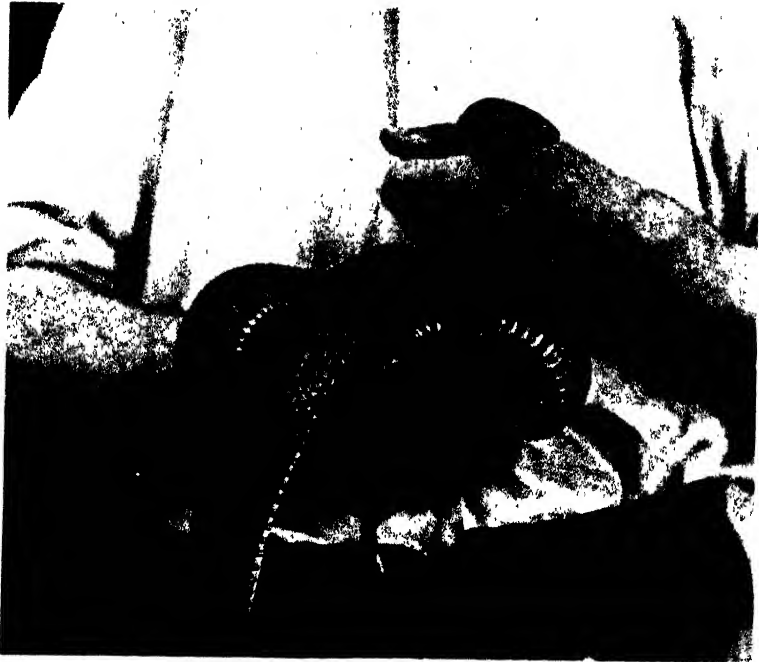


2.

Photo F. W. Olin

John B. A. Smith & Jan. 1924, L.V.





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Photo F. W. Ulrich

John Bale Sons & Dennison Ltd

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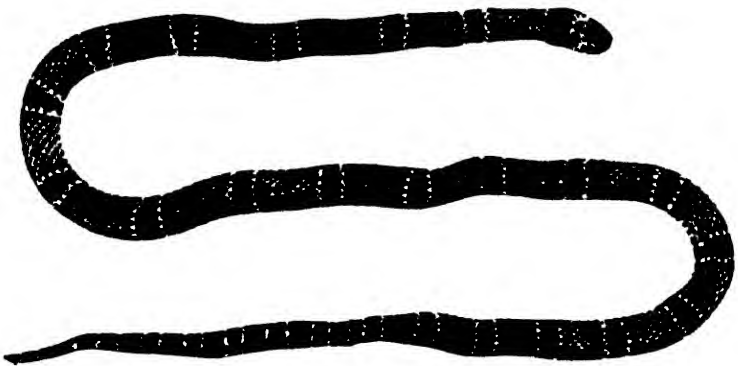
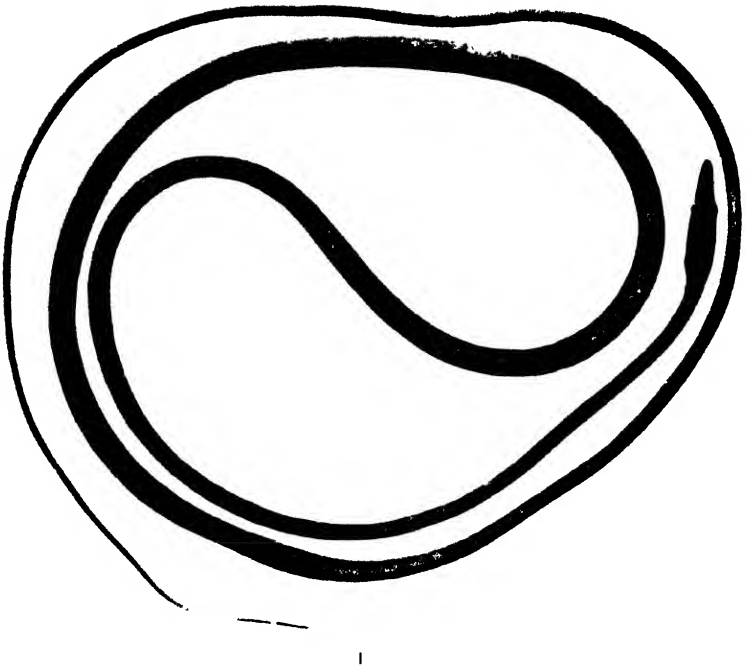


Photo R. W. Ulrich

2.

John Beie Sons & Daughters Ltd

TRINIDAD SNAKES





1.



Photo F. W. Ulrich

John Baird Smith & Danieleson Ltd

2.

TRINIDAD SNAKES

## 11. The Trinidad Snakes. By R. R. MOLE, C.M.Z.S.

[Received October 2, 1923. Read February 5, 1924.]

(Plates I.-X. \*)

Thirty-eight snakes are credited to the Fauna of Trinidad, British West Indies. Of these I have not seen three. They are: (1) *Typhlops reticulatus*, a very small reptile, only 300 mm. long, which lives in the earth and which is quite harmless; (2) *Boa diviniagua*, which is also found in Dominica and St. Lucia, and as many specimens from its other habitats have been under observation, in the proper place a short account of it is included in this paper; (3) *Lycognathus cervinus*. The last-named belongs to the Opisthoglypha, one or more of the posterior maxillary teeth being grooved. Most of the Opisthoglyphs are in a slight degree poisonous, paralysing before devouring the animals on which they feed. *L. cervinus* is said to attain a length of 930 mm. With these preliminary remarks, I proceed to describe briefly the snakes of Trinidad which have come under my observation during the years between 1886 and 1917.

## GLAUCONIDÆ.

## 1. GLAUCONIA ALBIFRONS Wagl.

This is a small snake, only 275 mm. long. Diameter of the body 45 to 55 times in the total length; length of tail 15 to 21 times. It has a conspicuous yellow spot on the forehead which becomes white in spirit specimens. Colour brown, lighter beneath, each scale with lighter outer edges, forming more or less distinct longitudinal lines. The tip of the tail is usually marked with a yellow spot. The reptile is a lively slippery creature, and looks as if made of polished steel. It may be found in the earth and under the bark of trees, and it has been taken in termites' nests. One captured in this last locality vomited several large termites. These snakes lay eggs, few in number, large in size, and elongate in form.

## BOIDÆ.

## 2. EPICRATES CENCHRIS.

Locally called "Mapepire velour" and "Jack." This reptile belongs to the subfamily Boinæ. In length it is about 1700 mm., including tail, which is 220 mm. The upper and lower labials have more or less distinct pits or impressions between them. The colour is a pale or dark brown, and there are markings in

\* For explanation of the Plates see page 278.

the form of rings and spots. There are five longitudinal lines on the head. The scales are small and smooth; the anal is entire, and the subcaudals are single—not in pairs. On each side of the anus there is a hook or claw. The head is small, though distinct from the round thick body. Seen in sunlight this snake is resplendent with a lovely iridescent peacock-blue. The very young ones are light grey, upon which the dark markings stand out prominently. *Epicrates* is invaluable to the agriculturist because, while harmless to Man, it is a deadly enemy to rats and mice, which it kills by constriction. It also preys on the smaller species of opossums (Manicou), birds, and bats; but mice and rats are its chief subsistence. A young one has been observed to swallow ten mice in two days. From time to time several have been taken in warehouses in Port of Spain. As many as 31 are produced at birth. "Jacks" have been seen coupling in October and January, and in the former instance the brood did not make its appearance until July.

### 3. *EPICRATES CENCHRIS* L., var. *FUSCA*.

In all particulars the same as the foregoing, except that the markings are very indistinct or faint.

### 4. *CORALLUS COOKII* Gray.

This is the unfortunate snake which in Trinidad is usually exhibited at carnival time. According to Dr. Boulenger, in his 'Catalogue of Snakes in the British Museum,' this reptile is 1550 mm. in length and its tail 320 mm. Specimens have been seen which were seven and even eight feet long. The upper labials are strongly pitted below and behind the eye, the anterior more or less distinctly pitted; the anterior lower labials are not pitted. The colour is pale yellowish or greyish brown above. The dark markings are variable and sometimes absent. There is usually one, sometimes two dark streaks behind the large and prominent eyes, of which (in daylight) the pupils are mere vertical slits. The head is arrow-shaped, the hinder part being much broader than the neck. The scales are small and smooth. The hooks, or claws, near the anus are well developed. Anal entire and the subcaudals single. Locally, in the environs of Port of Spain, *Corallus* is called "Cascabel," sometimes "Cascabel Dormillon," which has been said to mean "sleeping rattlesnake." In the centre of the island, and particularly at Arima, it is known as the "Mapanare," the term by which the Fer de Lance is identified in Venezuela; whereas, though exceedingly ready to bite when on the defensive, when it invariably draws blood, it is a most harmless and useful creature. It is in the wild exclusively arboreal in its habits, and feeds principally on rats and squirrels. It also on occasion devours birds. One specimen, recently collected, was constricting a bat. One of a

pair, taken *in coitu* by O'Reilly in February, gave birth to between 20 and 30 young in the following August. The individuals in every litter present wonderful variations in colour and markings, some having the pattern described by Dr. Boulenger, while many are of one colour (dark brown above and lighter beneath), and thus it is common to find brick-red, amber, yellow, and dark brown snakes in a single brood. The same species is also found in Grenada, where the markings are more uniformly pronounced, while the snakes generally are of smaller size. A wise planter will take care that the Castabels found on his property are not molested.

##### 5. EUNECTES MURINUS L.

The local name of this reptile is "Huile," and among naturalists "Anaconda." In South America it is the ophidian which attains the greatest size, and it is probably the largest of all the serpents. It is recorded that one killed near Irois (Trinidad) in 1810, or 1812, was 32 feet in length. This is quite possible, for there are museum specimens extant which are 33 feet. Much larger ones have been reported from time to time. The *longest* example I have seen was by no means the biggest. In the flesh it taped 17 feet 3 inches, but it only weighed 105 lbs. The *largest* I have seen was 16 feet 6 inches. It was brought from Guaico in a box, and was immediately weighed. Snake and case scaled 300 lbs. When the captive had been removed to more commodious quarters the container was put on the scales and was found to be 68 lbs. The animal was therefore 232 lbs., which far exceeds the weight of several 24-foot pythons of which there are records. The Huile is greyish brown or olive above, with a single series, or with two alternating series of large transverse blackish spots, and one or two lateral series of blackish ocelli with whitish centres. The top of the head is dark, and separated from the paler sides by a black streak on each side of the head and behind the eyes. The lower parts are whitish spotted with black. The markings are best visible in young snakes, the older ones being almost uniformly greyish brown. The scales are smooth, the anal entire, the anal hooks, or claws, are well developed, the subcaudals are in a single row—not paired. The adult anaconda lives in pools and sluggish rivers. One lived in such a locality in the village of Guaico, and was frequently to be seen on the bank basking in the afternoon sun, and the school children used to stone it from the opposite bank. It would disappear for quite long intervals, and then be unexpectedly found in its old haunt. Occasionally the young ones may be seen in bushes or on the branches of small trees in the vicinity of water. In Trinidad, besides Guaico, the anaconda is found in Cunapo, Sangre Grande, Manzanilla, Mayaro, and right away down south, and along the south coast to Cedros, and then north to within ten or twelve miles of San Fernando. These reptiles

have been observed to couple in December and January, both in and out of the water. During this act the anal hooks, which are hardly ever used, come prominently into play. The male throws a coil or two round the female, which is usually the larger of the pair, and his claws are moved quickly, and scratch the scaly sides of his mate, inducing her to crawl forward slowly until union is established. One pair was thus engaged from December 24 until January 13. The male was between seven and eight feet long, and the female was a fifteen-footer. The young are born alive in July or August, and litters have been counted which contained as many as 30 to 42 little ones. The anaconda feeds on rodents and almost any animal which comes down to drink of the water in which it is lying. They have been known to kill dogs and deer, and one which was in my possession voided the teeth of a large alligator and the great horny claws of a tamandua. One, at Cedros, was shot while constricting a sheep. I had a young one which vomited a small water tortoise. After this it is not surprising to learn that they will devour ducks and fowls. Though quiet and secretive in their habits, anacondas, when disturbed, are quite fierce. They are wonderfully strong. One was observed to leave the river at Cunapo, and to steal quietly towards the place where a man was cutting grass. Whether it intended an attack it is impossible to say, for the negro was warned in time. There is no doubt, however, that a sixteen-footer, if it threw its coils round a man, could kill him instantaneously by a single contraction of its muscles. An American collector, Mr. S. M. Klages, informed me that in Venezuela he saw a young Indian done to death in this manner. The snake had been caught, and the unfortunate native was playing with it and had placed it on his shoulders.

#### 6. BOA CONSTRICTOR L.

Popularly the Boa constrictor is supposed to be the largest of the ophidians, but, as a matter of fact, it only ranks fifth in the limited series of really great serpents. It is common everywhere in Trinidad, though seldom seen, and it is found in Tobago. The ordinary length is about eight or nine feet, but I have had in my cages two which were twelve feet long. Mr. E. L. Mirus, a Trinidad surveyor, assures me that he has seen one fourteen feet long. Hagenbeck, in his book 'Men and Beasts,' mentions one which was thirteen feet in length. Of course, one hears often of enormous ones seen in the woods and high bush. On one occasion the appearance of a giant macajuel (the local Creole name) was reported to me as having been seen crossing a track at Barataria. It was solemnly averred that the reptile was twenty feet long, and it extended from one side of the path to the other. I went to Barataria. The spot was pointed out and a search was made, and in the hollow trunk of a fallen palm-

tree three macajuel were found. They were an eight-foot female and two seven-foot males. The peasant had probably seen the inamorata closely followed by her suitors, and imagined that the three together were one huge snake, and it is easy to understand how he arrived at a length of twenty feet. Usually the *Boa constrictor* is a thick, heavy snake, especially if a female—the males are more lightly built. The coloration is pale brown, sometimes nearly black, above with 15 to 20 darker saddle-marks on the back. There is a dark brown streak on each side of the head passing through the eyes. There is a dark brown line from between the nostrils to the nape of the neck. The saddles on the tail are larger and frequently brick-red edged with black. On the upper-lip, below and between the nostrils there is a dark, crescent-shaped moustache mark. The belly is yellowish, and dotted or spotted with black. The anal is entire, the hooks are well developed, and the subcaudals all, or partly, single. It is a handsome reptile and, as a rule, of most quiet demeanour, and soon becomes tame and does not object to being handled. Macajuel feed on birds and small mammals. Sometimes they kill dogs. One slain in Maraval some years ago contained the body of a full-grown ocelot (tiger-cat), and Mr. Ulrich has a record of one which killed and devoured a full-grown mongoose. Macajuel also eat the large Teguxin lizards, locally called "Mats," and in captivity the young ones will greedily devour ameiva lizards. Ducks and fowls are also acceptable items in the Macajuel's dietary. They have been observed to couple in December, January, February, and March. In the males sexual excitement has been noted in October. Young ones have been born in May, and the largest litter recorded in my notes was 63. Macajuel hiss with open mouths, and the noise is something like the escape of steam from a small boiler.

#### 7. *BOA DIVINOLOQUA* Laur.

The local West Indian name for this snake is "Tête Chien" (Dog Head). In Dr. Boulenger's 'Catalogue of Snakes in the British Museum' it is recorded as occurring in Trinidad. The doctor's description is as follows:—"Total length 2100 mm. Tail 170. Snout rather prominent, obliquely truncate; rostral a little broader than deep; symphysial at least as long as broad; head-scales small, a little enlarged on the snout; no shields; one of the præoculars slightly enlarged; 18 to 20 scales across the forehead from eye to eye; 14 to 19 scales around the eye, which is separated from the labials by one or two rows of scales. Scales in 65 to 75 rows. Ventrals 258-275; anal entire; subcaudals single, 55-69. Brown or olive above, with 25 to 30 darker spots or cross-bands on the body, and a lateral series of spots and vertical bars with light centres; head-markings as in *Boa constrictor*, but sometimes rather



indistinct; the longitudinal line on the head broader, often interrupted or scalloped; tail black and yellow; lower parts yellowish, spotted and dotted with black or olive, sometimes entirely blackish."

I have never seen a Trinidad specimen of this snake. It may yet be found in some circumscribed locality such as the Northern Hills, or between Moruga and Point Galeota on the southern coast. I have seen many specimens from St. Lucia and Dominica. Generally they were about the size of *Corallus*, though rather stouter in build. They reminded me of that reptile and also of *Boa constrictor*, but they have none of the peaceableness of the latter, and are even more irascible than the first-named. They continually snap at passers-by, regardless of the fact that they are not near enough to get a bite home. Confined in a small box, they ruin themselves by breaking their noses on the glass front. Whether this is the natural disposition of the animal I do not know. Perhaps the adults I possessed were used roughly when they were taken. Even then the young ones born in captivity are as cross and pugnacious as their parents. Six adults which came to me from Dominica had had portions of their tails cut off, but the scars had healed nicely. The majority of the specimens I have seen are very like small *Boa constrictors* in general appearance. They are more tree-loving in their habits, and in that respect are more akin to *Corallus cookii*. Several litters were born in my cages, but the broods were never large, not more than nine or twelve, and on one occasion there were only three. Some of them fed readily enough on rats and mice, but all died in a short time. My impression is that they prey principally on birds and lizards—possibly iguanas. At any rate they require a variety of food. My most successful example, born in my cages, fed on mice and lizards given to it alternately. By the more enlightened planters in St. Lucia these snakes are considered valuable because of their rat-devouring habits. It should be mentioned that they vary considerably in coloration, and some of them, for the greater part, are shining black, relieved by yellow marking and tracing.

#### COLUBRIDÆ.

Series A. *Aglypha*.—Solid teeth, not grooved.

#### Subfamily COLUBRINÆ.

##### 8. *HELICOPS ANGULATUS* L.

This is a small harmless snake which, because of its keeled or carinated scales, colouring, and marking, presents a superficial resemblance to the justly-dreaded *Lachesis mutus*, is locally called "Water Mapepire." It passes most of its life in ponds, ditches, and slowly-running streams. It is a stoutly-built creature,

about 730 mm. long, of which 200 mm. belong to the tail. The tail-scales are strongly ridged. The colour-pattern is yellowish green; across the back there are from 35 to 43 dark green, black-edged bands, broad on the spine and narrowing as they approach the under surface. The small eyes are placed so that they look upwards. Some specimens have brick-red bellies with dark spots. The anal is divided and the subcaudals are in pairs. When taken from the water these snakes frequently coil, and at the same time flatten themselves, throughout the body-length, in a most extraordinary fashion. When in this position they will spring vertically quite a little distance, at the same time attempting to bite. Probably the reason for this action is to deter herons and other birds from attacking them. The upward jump must be sufficiently disconcerting to the enemy to permit the snake escaping by diving deep into the mud or grass under the water. *Helicops* feeds on frogs and fish, and may often be observed controlling the struggles of its victims by throwing tight coils round them. Captain Ulrich has a fine specimen which was caught when trying to take a live fish from a hook. Of *H. carinicauda*, indigenous to the Grande de Sul (Brazil), Mr. Lydekker ('Royal Natural History') says that it produces living young, which is the rule with water snakes. It may be that the Trinidad *Helicops* is the exception. Mr. R. L. Ditmars, author of 'Reptiles of the World,' in a letter, dated October 1906, says of one that I sent to him, that it laid eight eggs on the voyage.

#### 9. STREPTOPHORUS ATRATUS Hallow.

Length 360 mm., which includes the tail, 60 mm. There are four well-marked varieties of this reptile—A, B, C, D; and B seems to be the Trinidad snake. The scales, which have apical pits, are more or less strongly keeled. The anal is entire and the subcaudals are in two rows. The animal is dark brown or blackish above, with a more or less distinct yellowish collar or occipital blotch; belly yellowish or brown, sometimes dotted with a deeper brown. This snake has simply been collected, and, so far as I know, no observations have been made upon it. The first I saw was taken by Mr. Broadway, who got it in a bamboo clump. Only two or three specimens have come my way.

#### 10. DRYMOBIUS BODDAERTI Sentz.

This is the "Machette Couesse" of the Trinidad peasantry. The scales are smooth and the ventrals are obtusely angulate; the anal is divided and the subcaudals are in pairs. In colour this snake is brownish, greyish, or olive above, uniform or with a pair of light streaks along part or the whole of the body. Those found on the mainland of Trinidad invariably have these streaks, and so too have those taken on the island of Gasparee,

which is only a mile distant. But those observed on Patos Island, eight or nine miles away, and about three miles distant from the Venezuelan coast, do not seem to have these ornamentations, and I believe I have heard that the same peculiarity characterizes the Couesse found on Chacachacare. Sometimes the scales are black-edged. There is a more or less distinct dark streak on each side of the head. Belly yellowish, uniform or dotted with olive. Sometimes the throat is spotted or marbled with brown. When young the Couesse is prettily mottled, the uniform greenish brown or olive of the adult being embellished by darker cross-bands, which are broken at the sides and end at the ventral scales. Towards the posterior end these markings become fainter, and ultimately cease altogether at the junction of the body and tail, the latter being of the colour the snake will wear during adult life. The change from the finery of extreme youth to the sober livery of adolescence has been observed in my cages. This snake attains a total length of 1090 mm.; tail 310 mm. In the adult the tail is seldom of natural length, probably because its owner is a great hunter of mice and other small mammals, and loses bits of its caudal appendage in its fights with its victims. The Machete Couesse used to be commonly found in the Botanic Gardens in Port of Spain and the vicinity, and as often in the bushes as on the ground. It is an expert climber, and if it is more rare than it used to be (and I am told that it is), and if it has not been killed out by the Mongoose, it has probably taken altogether to an arboreal life in Trinidad. Its food consists of frogs, lizards, and birds. Mice excite these reptiles to a perfect frenzy, and they dash after them with a determination which ends badly for the fugitives. Sometimes the victim is seized by the head, and then the process of swallowing begins at once. On other occasions it is caught by the fore- or hind-leg, and then, regardless of all bites and struggles, the snake holds on like a bulldog until the captive is dead; or, if the reptile is strong enough to do so, it passes the wretched mouse through its jaws until it reaches its muzzle, when deglutition commences forthwith. The Couesse has been observed nosing about amid sticks, stones, and leaves, showing great activity and alertness. On one such occasion a cricket was disturbed, and got away by great jumps. At every leap the Couesse rushed forward with accelerated speed, but it was not observed to capture the insect. Taken in the hand, the newly-caught Couesse bites with determination, viciously working the tiny teeth into the skin. Of course they hardly draw blood. These snakes are snappish and pugnacious. When excited they rapidly vibrate their tails, tapping the ground, or leaves, and making a noise not unlike the alarm of the rattlesnake. The breeding-habits are unknown, but it is believed that they are produced from eggs, which are laid in masses of moss or leaves.

11. *PHRYNONAX SULPHUREUS* Wagl.

So far as is known, there is no local name for this comparatively rare, large, and beautiful snake. Total length 2700 mm.; tail 720 mm. Scales, except the outer rows, strongly keeled. Ventrals strongly angulate; anal entire; subcaudals in pairs. In colour this handsome ophidian is yellowish, olive, or brown above, with irregular oblique cross-bars which are sulphur-coloured, wherein it resembles the "tigre" (*Spilotes pullatus*), to be described later, only the stripes are not pale yellow. The hinder part and the tail are blue black. Few specimens have been examined, and it may be considered rare in Trinidad; at least it is not often seen, as it probably spends the greatest part of its life in the high forest-trees. It angrily and vigorously resents interference. On such occasions it inflates its neck, when it looks as if it were swallowing a large egg. It also vibrates its tail. Specimens in captivity have willingly fed on mice, young rats, and ground-lizards.

12. *PHRYNONAX FASCIATUS* Ptrs.

This is a rare snake; at least very few have come under my notice. Total length 1500 mm., of which the tail takes 400 mm. The scales on the back are faintly keeled; the ventrals are obtusely angulate. Anal entire; subcaudals in two rows. The adults are uniformly dark olive-brown. The young ones are pale brown, with crescentic brown, black-edged cross-bands; head pale brown, speckled with a darker tint; belly closely speckled or powdered with brown. The first specimen I saw came from Carenage. It was examined and identified by the late Dr. Boettger. Many years afterwards I saw a snake which came from Cunupia and which I believe was of the same species. This snake agitates the tail when excited.

13. *PHRYNONAX EUTROPIS* Blgr.

The local name is "Cutlah." The dorsal scales are strongly keeled, the ridges forming continued raised lines in the middle of the body. The ventral scales are obtusely angulate. Anal entire, and the subcaudals are in two rows. In colour this reptile is uniform brown above, upper lip and anterior lower surfaces yellow, the belly turning to olive-brown towards the tail. For many years the habitat of this snake was unknown, and the single example in the British Museum was figured in vol. ii. of Dr. Boulenger's 'Catalogue of the Snakes in the British Museum.' The specimen which established this species in the Trinidad fauna was crossing the road near Maraval Waterworks, when it was taken by Mr. Alec Hamlyn and the late Mr. John Hoadley. Another was subsequently taken a few miles away at Santa Cruz. Two or three have been collected at Caparo, and during 1913-14 several were caught at Cunupia. I got one at Mayaro Point. It is therefore, although not numerous, widely

distributed in the island. It is a fierce and irritable creature. I have never been able to induce it to feed. Mr. J. O. Dolly, of Mayaro, who says that it is comparatively common on the east coast, tells this story. He saw a Cutlah beneath a bridge, where it was devouring a mouse. A larger mouse attempted to rescue the victim, and courageously bit the snake several times. The serpent, violently agitating its tail, persevered with its meal, and finally swallowed it, whereupon the would-be saviour retreated to an adjacent hole, whither it was quickly followed by the Cutlah.

#### 14. SPILOTES PULLATUS.

In Trinidad there are two varieties of this large and beautiful snake. The most common and handsome is black with several broad, pale yellow oblique cross-bands on the fore part of the body. The posterior portion and the long tail are shining black, and underneath bluish black. The anterior part of the under surface, including the throat, is yellow, with black spots or bands. The scales are keeled, strongly imbricate, acutely pointed, and have apical pits. The anal is entire and the subcaudals are in two rows. The rarer variety is in most respects like the first one described, but the yellow bands are reduced to a few irregularly-disposed spots, and the anterior ventral scales may be partly yellow. When this snake is well marked with yellow the country people call it "Tigre," and when it is nearly all black it is a "Tigro," when, because of its sombre livery, it is to be carefully avoided, although both kinds are said to be dangerous. Both varieties are credited with chasing intruders and generally behaving in a most truculent and reprehensible manner. I once heard of an instance which shows how such stories originate. A man was going up a steep ravine, or water-course, which are numerous in the hilly parts of Trinidad. He heard a rustle and saw a large Tigre. A snake going downhill sometimes attains a high rate of speed, and this one was coming at a great pace. It had probably never seen the man, who turned, uttering wild yells as he ran. His adventure is cited as proof positive of the ferocity of the Tigre, though why a snake should not toboggan in its own domains, without being intent on mischief, no evidence has ever been forthcoming. When cornered, the Tigre will stand up to a man, prepared to sell its life as dearly as it can. It will inflate its neck, like *P. sulphureus*, and dart at the enemy open-mouthed. But it is a harmless beast, and it is to be doubted whether it will ever bite until it is actually handled. When it does bite, it bites quickly and hard; but the injury, at the worst, is only a few scratches. If the bitten one exercises sufficient self-control and does not snatch his hand away, there will not even be scratches—only a few blood-drops from the punctured wounds inflicted by the small non-venomous teeth. In an hour one will have to

find the site of the injury with a magnifying glass. It is not known whether the adult Tigre feeds on either lizards or frogs—creatures which should be rigidly protected, but that he kills a large number of mice, rats, and possibly squirrels there is no doubt at all. Some birds enter into his dietary. The prey is killed by constriction, but mice are swallowed alive. A young Tigre would not feed, but he would savage a finger if he could lay hold of it. I took advantage of this trick, and instead of the finger presented him with a dead mouse to worry, which he would do as long as he was held. The result was that the mouse was invariably swallowed, to the snake's great benefit, and thereafter he was successfully fed in this fashion. The yellow Tigres are not nearly so common as they were. The last really typical specimen I saw had ten well-defined broad pale yellow stripes on the fore part of the body and two imperfect ones about the middle, while the hinder part and tail were an intense blue-black. This snake vibrates the tail. It is mostly found in trees. Caged together this species and the previous one (*Phrynonax eutropis*) have been observed to couple. The Tigre may attain a length of 2100 mm., including the tail, which is 490 mm.

#### 15. COLEBER CORAIS Boie.

This snake is locally known as the "Cribo," or "Clibo," and the older generation of Trinidadians will hardly need any description of what was once a very well-known reptile. Of late years it has become exceedingly rare, or, at any rate, few are now met with. Whether the advent of the Mongoose has induced it to become almost entirely arboreal in its habits is a matter for conjecture. Country people and others whose business takes them afield, and naturalists, have informed me that they have not seen a Cribo for many years. The Trinidad Cribo is a strongly-made and active animal, greyish black in colour, with a yellowish-brown tail, which gets brighter towards the extremity. The plates on the head are tawny, and those on the lips are edged with black. The scales are smooth or with a short feeble keel. The anal is entire and the subcaudals are paired. The length may be 1880 mm., of which the tail is 400 mm. Count de Verteuil, in his book on Trinidad, says that they may be seen twelve feet long. I have seen one nine feet, and then some inches of the tail were missing. But during many years the average length of those which came under my observation was about four or five feet. The Cribo moves at a smart pace in bold, graceful, and continuous curves, and it climbs and swims well. When captured or cornered it turns fiercely on the aggressor, and, with inflated neck and open jaws, strikes boldly and bites hard, at the same time emitting a most offensive odour. These snakes are susceptible to kind treatment, and if accustomed to gentle handling, they soon discard these habits. Their eggs

number nine to twelve in a clutch. The Cribos is practically omnivorous, devouring everything it can swallow, but it discounts its usefulness as an inveterate mouse and rat destroyer by also preying upon frogs, lizards, small birds, and stray chickens. If a hen has a brood and there is a large Cribos in the vicinity, it will rush boldly into the chirping covey and take a chicken every day, so long as it is convenient to do so. When it has had four or five, it will probably lie up for a week, when, like all other snakes, it will become partially blind, its eye-scales turning bluish white, while its livery will be dingy and without lustre. After a day or two the snake's eyes will regain their wonted colour, and then their owner will go into some hedge or into long grass, and rubbing its nose and lips against any rough surface it may find, its old skin will turn back from the mouth. It will go on pushing and rubbing, and the slough will continue to turn back, the scales covering the eyes will come off with the rest, and the reptile will finally literally walk out of its old habit, leaving it reversed like a glove, and in the glory of a perfectly-fitting and not unhandsome suit of new clothes, it will look round to see if that old hen has any more stray chickens which she cannot take care of. The Cribos has been observed to catch fish, and there is a record of one actually being seen in the sea close to the shore and capturing a young grouper. The Cribos makes its meals on the "quick-lunch" principle, grabbing its prey anywhere and swallowing it at once, and disregarding even the bites which the rat may inflict upon its destroyer. In consequence, old snakes are frequently much scared. Cribos also devour other snakes, even poisonous ones, but further investigation is required on this point, for Cribos, like other non-venomous colubrids, may be immune to the bites of the vipers (the mapepires), though they may not, with them, be able to resist the poison of the dangerous colubrids—*Elaps* (Corals).

#### 16. HERPETODRYAS CARINATUS L.

The local name of this most beautiful snake is "Yellow Machete," and though it is most often found in trees and high bushes, "Machete Savanne." It is a large-eyed species. The scales are smooth except the two middle rows on the spine, which in the female are faintly keeled and in the males strongly carinated. The length is, or it may be even more, 1530 mm., of which the tale is 500 mm. It is dark brown above, but it has a large amount of yellow on the sides. The ventrals and subcaudals, the latter of which are paired, are yellow with black edges. There is also a variety in which green appears on the back. The anal is divided as a rule, but there are instances in which it has not been divided. I have captured them in trees, bushes, pools, and on one occasion, after a long and exciting chase, caught one, which was first seen crossing the drive to the Governor's house, in the Botanic Gardens, Port of Spain. On the Caroni River on one

occasion a large female, attended by two males, was observed on a small thorny tree. They successfully eluded all attempts at capture. When annoyed these snakes inflate the anterior portions of their bodies so that the dense dark colour of the back and upper sides is varied by the appearance of the pink skin between the scales. This snake bites quickly and fiercely, and it also lashes with its flexible tail. Machetes may devour birds and mice, and most likely do so, but in captivity they appear to care only for frogs, which they swallow eagerly and in rapid succession. Little is known of their breeding-habits, but one has been observed to lay five white, parchment-like covered eggs, each of which was two inches long and about as thick as the little finger. The Machete when angry or excited is another of the snakes which agitates the tail.

#### 17. *LEPTOPHIS LIOCERCUS* Weid.

Locally known as "Lora" or "Parrot Snake." This slender little reptile may attain a length of 1720 mm., of which the tail is 590 mm. The ventral scales are decidedly angulate laterally; the anal is divided; the subcaudals are in pairs. On the body, except the outer ones, the scales are strongly keeled. The colouring is bronzy or golden above, and usually the vertebral region is green, and there is a dark streak passing through the eye on each side of the head. The lower parts are white or yellow. The Lora used to be common in country gardens in the suburbs of Port of Spain, and Scarborough—Tobago. When excited the snake slightly inflates itself, and the gold and green on the neck and the anterior part of the body become brilliant. The head is rather large, and the angry snake widely opens a big shell-pink mouth, laterally spreading the back part of its head, but it rarely bites, and when it does so the wounds are quite small if they are inflicted with the more forward teeth. The back teeth are rather long. In the human subject the after-effect of the teeth is a stinging sensation which passes off in a few moments. Loras are usually found in trees and bushes, and only occasionally on the ground. They are rapid and graceful in their movements. Their diet is frogs and lizards and possibly young birds. Although the Lora belongs to the Aglypha, having solid teeth and is not poisonous to human beings, it has been noticed that small lizards which have been wounded by the Lora's back teeth, and have afterwards escaped, soon die of their injuries.

#### 18. *LIOPHIS MELANOTUS* Shaw.

Total length 610 mm., tail 140 mm. The head of this little snake is greenish bronze. The back, right away to the tip of the tail is black, forming a broad stripe four or five scales wide. Then on each side is a yellow stripe two scales wide, also running the whole length, and this is accentuated by another



black stripe on both sides, with a yellow and black alternating stripe, about half a scale wide, on the lower edge. This is followed by another stripe on each side, of a pale salmon tint. The under parts are yellow, the edges of the scales being lined with bluish black. The broad black stripe on the nape and the first third of the length is flecked with golden yellow. There is a black streak on the upper labials from the nose to the beginning of the yellow streaks on the sides. The scales are smooth. The anal is divided and the subcaudals are in two rows. This is one of the commonest ophidians in the colony, and most people know it. The Creoles call it "Beh Belle Chemin"—"Beauty of the Road," and it is indeed a beautiful little creature. It feeds on little frogs and lizards, and in its battles with these creatures it tightly constricts them in its coils. These snakes enter water, and will catch small fish. At times they will remain for days in the bath. They have never been known to bite, but they flatten the first part of the body when alarmed. They have considerable climbing powers, and are most active little creatures. In the month of June one specimen laid seven eggs, which were white and covered with a tough, parchment-like skin.

#### 19. *LIOPHIS REGINÆ* L.

This extremely beautiful snake owes its second scientific name to the fact that it was dedicated to a Queen of Sweden. Locally it is called the "High Woods Coral." The word "coral" is in Trinidad usually applied to the venomous *Elaps*; but this snake is not poisonous. A large one is 650 mm. long, of which 165 mm. belongs to the tail, which is often mutilated. The adults are olive or greyish yellow, with the edge of each scale black. They look as if they had pieces of black mosquito curtain strained over them. The young have a yellowish collar and an oblique yellowish, black-edged band on each side of the head. The belly is yellowish with numerous black spots. It is a comparatively rare serpent. The only specimen observed fed well on frogs and lizards, and it would go into the glass jar to catch little fish. It flattened its head and neck when irritated. It is said to be found in the vicinity of mangrove swamps and streams. The anal is divided and the subcaudals are in pairs. The scales are smooth.

#### 20. *RHADINÆA COBELLA* L.

Length 730 mm., of which the tail is 125 mm. The anal is divided and the subcaudals are in pairs. If coloration makes variety, then there are two kinds of this snake in Trinidad. Years ago I thought the specimens mottled with black, olive-brown, and dirty yellow, with grey scales on the lower jaw, were males; but one of this coloration laid eggs. The other variety's colour-scheme is marked by faint transverse stripes on the back, caused by the arrangement of smooth slate-coloured scales with grey edges. The ventrals are chequered with large black spots on the white

surface. Sometimes these snakes are three feet long, but the average size is about eighteen inches. The Creoles call it "Mapepire Mangue," or "Mangrove Mapepire" and "Mangrove Snake." It is found in swamps and sometimes in brackish water close to the sea. It devours large numbers of frogs, and once a specimen was observed to swallow a gecko. It also catches and devours fish. Young ones have been observed in June. One of these snakes laid several eggs in my cage. Only one hatched, and the product was black and deformed, refused to feed, and soon died.

#### 21. *HYDROPS TRIANGULARIS* Wagl.

Length 780 mm., of which the tail is 110 mm. Purplish brown above, red on the sides, white below. Black rings or annuli, which may be interrupted and alternate on the middle dorsal and ventral lines. The scales are short and smooth. The anal is divided and the subcaudals are in two rows. This is a water-loving little snake, and the Creoles call it the "Water Coral." The late Mr. J. T. Thorpe brought the first I received, and he got it at Arima. Others have come from the Caroni swamp. One was taken in Princes Town by Mr. F. W. Urich. Another was caught at Four Roads. A collector once brought fifteen of all sizes from Cunupia. It is a reptile which does not do well in captivity. It has been observed to devour little fish. It has a great objection to staying in the same tank with *H. angulatus*. The body is ringed something like the coral—an ophidian which it resembles in build,—but the rings are not like those of the venomous coral snake in either colour or shape; they are much closer together, are more regular, and are black or dark slate in colour.

#### 22. *PETALOGNATHUS NEBULATUS* Wagl.

The Creoles call this snake "Mapepire Corde Violon," or "Fiddle String Mapepire," a name which surely applies more accurately to another species to be mentioned later on. Its length is 790 mm., of which 210 mm. is tail. The scales are smooth, the anal is entire, and the subcaudals in two rows. Above, the colouring is grey or grey-brown, with blackish spots; or it may be mottled black and white with more or less regular cross-bars, which may have a light edge. The belly is yellowish, with black dots and more or less regular cross-bars, or large alternating spots. The head is shortened, flattened, and rounded, and the eyes are very prominent. When molested this snake draws back its head in a most threatening manner, and even strikes, *but with closed jaws*. Being locally called a "mapepire," it is treble damned as a wicked and venomous serpent. As a matter of fact it is retiring in its habits, and only ventures out at night. It spends its days rolled up in the cup-like bases of wild pines, in bushes, under fallen leaves, or in decaying vegetation. When

active, it goes slowly and cautiously about its work of slug-destroying. It is therefore the friend of the gardener, but, unfortunately, when found it is almost always slaughtered for its pains. It is curious to see *Petalognathus* capturing slugs. When the snake, in its rambles at dusk, sees a mollusc it at once becomes interested. It raises its head and looks fixedly at it. With arched neck it approaches slowly to the victim. Then it suddenly darts forward and seizes the wretched snail between its horns. It is difficult to follow the motion, which is very quick. The result is that the greater portion of the slug is immediately in the snake's throat. It is remarkable how small is the quantity of slime exuded by the slug, though the prey is not always attacked between the horns. Several of these snakes have laid eggs in my cages. They are white and, like those of other snakes, are rather long and covered with a tough envelope. This reptile is afraid of other snakes, and does not appear to be interested in much else save slugs.

### 23. *ATRACTUS TRILINEATUS* Wagl.

Length 225 mm., of which the tail is 15 mm. This reptile is brown or greyish above, with three or four darker longitudinal lines. It is sometimes spotted. Underneath it is yellowish white. The subcaudals are paired and the anal is entire. Locally it is called the "Ground Snake." It is often found in rubbish-heaps or in the earth. It is perfectly harmless, and possesses a small head and short tail. Coral snakes prey upon them and, unfortunately, what specimens came to hand were always wanted to feed *Elaps*. The species lays three or four eggs at a time, and they are large compared with the size of the parent. It is an ophidian which devours insects, and may be regarded as the friend of the gardener.

## COLUBRIDÆ.

Series B. *Opisthoglypha*.—Most, if not all, of the snakes in this division are poisonous to a slight degree. One or more of the maxillary teeth are grooved.

### 24. *TRYPANURGUS COMPRESSUS* Daud.

I have only seen one specimen of this snake. It was taken alive in April or May 1914 by a man of the Forest Reserve at Sangre Grande, and was lying under a heap of leaves. The only men who know the Trinidad Ophidia, Mr. F. W. Ulrich and Mr. A. B. Carr, had never seen it before, and though I made many inquiries, no one else seemed to be acquainted with it. Its long tail and compressed form lead one to the supposition that it is a species which inhabits that strange world to human beings, the high forest trees, and that, oppressed by the long drought, this particular specimen had been forced to seek the earth to obtain

moisture. It only fed once, and then on an anole lizard. The head was blunt and distinct from the neck, and evoked reminiscences of *Petalognathus*, *Himantodes*, and rather less of *Leptodira*. The eyes are prominent, ruby-red, with elliptical pupils placed diagonally. Over the eyes and the muzzle there was a dark shade of brick-red. The hinder part of the head was a lighter hue. Two inches behind the head was a blotch of dark grey. The ground-colour of the remainder of the body was dull red. From the grey blotch to the tip of the tail was a series of fifty-four thin dark grey saddle marks, sometimes broken on the back, in other cases alternating, and occasionally mere spots. The under side was pearly white. In the notice of the species in the 'British Museum Catalogue of Snakes' the length is said to be 1100 mm., of which the tail is 340 mm. The vertebral scales are strongly enlarged, and the biggest broader than long. The scales are smooth, with apical pits. The anal is divided and the subcaudals are in pairs. In the Trinidad specimen the length was 51 inches; the ventrals numbered 264. The subcaudals were 124 pairs.

## 25. HIMANTODES CENCHOA D. & B.

This peculiar, very beautiful and inoffensive reptile attains a length of 1100 mm., of which the tail takes up 340 mm. The scales are narrow, smooth, with apical pits, those of the spine being strongly enlarged. The anal is divided and the subcaudals are in pairs. The head is blunt, the muzzle being short, and the occiput is much wider than the slender neck. The eyes are prominent. There is a "Y" mark on the head, the prongs of which begin behind the eyes. The colour-scheme is pale brown or greyish, with numerous darker saddle marks extending the whole length of the snake. In some places these are continuous, while in others they are disjointed, the lighter tint interrupting it. The lower surface is dotted with brown, and sometimes there is a median line. The body is triangular and so attenuated that it is semi-transparent. The tail ends in a fine point. Locally this snake is called "Mapepire Corde Violon," or "Fiddle String Mapepire." I have never known these snakes attempt to bite. They coil up into a very small space, and so are able to conceal themselves most effectively in orchids and wild pines, situations where they may frequently be found. They used to be rather common among the orchids at the Colonial Hospital. Only once have I seen one on the ground, when it was entering a clump of high grass. On one occasion Mr. Rorer found one in his waste-paper basket. This snake is almost entirely nocturnal in its peregrinations. By day it is in the habit of concealing itself, but at night it gracefully glides about and bridges considerable distances between branches, only supporting itself by a small portion of the body and the long tail. It feeds on gonatodes (the small striped lizard) and garden anoles.

26. *LEPTODIRA ANNULATA* L.

This is another innocent which has been damned locally by being given a name which also applies to a really dangerous creature. It is called "Mapepire Valsyn," or "M. Balcyn," or "M. Barcin." Its length is 730 mm., of which the tail is 175 mm. The scales are usually smooth or only faintly keeled, and they are pitted apically. Those along the spine are sometimes larger than the others. The anal is divided and the subcaudals are in two rows. The colour is yellowish, or brown above, with a dorsal series of large dark brown or blackish spots, which are continued to the ventrals. Sometimes the black spots form an undulating streak on the spine. The under parts are whitish. The head is distinct from the neck. The eyes are large. When molested this snake draws back its head as if about to strike, but seldom, if ever, makes any attempt to attack the aggressor. It frequents outhouses, old walls, and rubbish-heaps. Once one was taken in the bough of a tree, where it shared its quarters with a large colony of ants. *Leptodira* feeds on frogs and small lizards. It lays eggs, but the only one which did so in my cages promptly devoured the whole clutch. These snakes are very local in their habits, never going far afield. One escaped and was gone for months. In the meantime the family moved to another house on the other side of the town, and there the missing pet turned up. It is supposed that it had been carried in some article of furniture to the new quarters.

27. *OXYRHOPUS PETOLARIUS*.

This snake is the latest addition to the known ophidian fauna of Trinidad. A young specimen was obtained in 1914 or 1915. It came from St. Joseph. Adults were received from Cunupia in 1916. Since then others have been received from River Estate, Diego Martin. In volume iii. 'Catalogue of the Snakes in the British Museum,' by Dr. G. A. Boulenger, it is thus described:—

"Eye moderately large; its diameter about half the length of the snout, which is rounded and scarcely projecting. Rostral broader than deep, just visible from above; internasals much shorter than the præfrontals; frontal once and one-fifth to once and one-third as long as broad, as long as its distance from the end of the snout, as long as or a little shorter than the parietals; loreal much longer than deep; one præocular (sometimes divided) usually forming a suture with the frontal, sometimes however narrowly separated from it; two (exceptionally one or three) post-oculars; temporals 2+3; eight (exceptionally nine) upper labials fourth and fifth (or fifth and sixth) entering the eye; four or five lower labials in contact with the anterior chin-shields, which are as long as or shorter than the posterior. Scales in 19 rows. Ventrals 191-222; anal entire; subcaudals 78-126 pairs. Coloration variable. Total length 910 mm.; tail 220."

Apparently there are two or more colour-variations in Trinidad, and therefore it is necessary to quote the paragraphs in the 'Catalogue' which describe them:—

"(a) Black above, with numerous (50–75) narrow yellow cross-bands, the first on the nape (*C. petolarius* L.).

"(b) Light cross-bars (sometimes reduced to large spots) on the side fewer (15–25) and far apart.

"(c) Uniform dark brown above, or with faint traces of light bars as in (b).

"(d) Above barred black and red; the red bars, which may be dotted with black, as broad as or a little narrower than the black, and thirty to forty in number; the black bars usually forming complete annuli on the tail."

The first specimen (in spirit) received was the one depicted in the photograph No. 1. It was quite a small snake. The second, taken while the snake was under the influence of chloroform, is the subject of the second photograph. This last was a black snake, with faint oblique bars on the anterior part of the body, and they could be seen in strong sunlight. It was a long time before it was discovered upon what this one and others of the same species fed. At last it was found that they would eat mice, and, singularly enough, they did not object to them when dead.

## 28. *OXYRHOPUS CLÆLIA* Daud.

This is a most valuable snake, but unfortunately not too common. It is not nearly as prolific as the dangerous ones upon which it feeds. A Fer de Lance produces commonly as many as thirty highly venomous young, fully developed and ready for the business of life, whereas this *Oxyrhopus* only lays about sixteen white eggs, which in place of a shell are covered with a parchment-like envelope. Locally this timid night serpent is known as the "Black Cribo" and "Vidua." In Brazil it is called the "Mussuruna," and this last is the name by which it will be referred to throughout this notice. In the 'Catalogue' it is stated to be 1550 mm. in length, of which the tail measures 340 mm. But the same authority also states that there is a larger one in the British Museum which measures 2100 mm. to the vent; the tail is injured, probably abbreviated. At the highest point on the Saddle Road I personally found one, which was over six feet long, dead. There are records of still larger ones. The scales are smooth, with apical pits; the anal is divided; the sub-caudals are paired. Superficially the Mussuruna may be described as a large blue-black reptile, with a pearly-white under surface, which is mottled under the tail. It is a powerfully-built animal. When taken in the hand it does not usually attempt to bite, but binds itself strongly round the wrists of the aggressor, and so tightly as to stop the circulation. It does not seem to be able to see well except at night. It has long been known as a slayer and devourer of venomous snakes. The Count de Verteuil, in his book on Trinidad (published in 1856), relates how some

years previously the late Mr. Robert Mitchell, Protector of Immigrants, at Blanchisseuse saw one killing a *Trigonocephalus jararacu* (Fer de Lance), and it had already swallowed twelve inches of the enemy when Mr. Mitchell arrived on the scene. Prof. Carmody took one which was killing a tree boa almost as big as itself. Mr. Albert Carr saw one killing a Tigre. I have myself seen a Mussurana kill and swallow a Fer de Lance which was only an inch or two shorter than itself. Subsequently I saw the same snake kill and devour several other venomous serpents. As a matter of fact, the Mussurana is invariably found in the localities frequented by dangerous ophidians. Mr. Ulrich caught a Mussurana in the northern hills, and in two months within six hundred yards of the spot his men killed twenty-three Fer de Lance. The Mussurana quickly seizes a Mapepire at the nearest possible place. The doomed snake turns and buries its long poison-fangs in the body of its destroyer, which, however, does not notice the incident, but, if the victim is a large specimen, throws numerous constricting coils round it and promptly crushes it to death. If small, and therefore easily managed, the Mussurana passes the Mapepire through its jaws without letting go, and, when reaching the head, commences to swallow the vanquished one. Dr. Brazil, the author of 'La Defense Contre l'Ophidisme,' who has made a great study of the snakes of Brazil, has everything that is good to say of the Mussurana as the destroyer of the terrible pit vipers of South America, but adds that while it is immune to their potent poison, the snake succumbs to the bite of the venomous coral snakes (*Elaps*). The reader is specially referred to the photograph illustrating this most valuable snake\*.

## 29. OXYRHOPUS CORONATUS.

In the 'Catalogue' the length of this snake is recorded as 870 mm., of which 200 mm. is tail. It is also stated that there is a much larger specimen with an injured abbreviated caudal appendage which measures 1060 mm. to the vent. The average specimens I have seen were about forty inches long, but a few have been even larger. The scales are smooth, with apical pits. The anal is entire and there is a single row of subcaudals. The coloration is reddish, or pale brown to blackish above, and paler brown or yellowish on the sides. The upper surfaces of the head and nape are blackish. Young ones are coral-red and wear a yellowish-white collar. Locally this snake is called "Mapepire Velour" and "Ratonero." It is frequently found under houses in Port of Spain, and at night it used not to be an uncommon occurrence to see one either in the gutters or crossing the road. Some years ago, in two nights five specimens of good size were taken in the roads in Victoria Square, where an old hedge had been grubbed up. The Ratonero is remarkable for its smooth, shining coat of mail. It is seldom seen in the daylight, but when

\* See Plate VIII.

it is moving in a strong light, many beautiful prismatic colours appear on the scales. Ratoneros are mouse-, lizard-, and frog-eaters, and in their battles with the rodents often lose portions of their tails. The Ratonero is short-sighted, and usually gets its prey by following it into its subterranean retreats. It constricts both mice and lizards. It also eats other snakes, and is frequently a cannibal in that it preys on its own species. Two Ratoneros when offered some young *Fer de Lance* declined to notice them. Ratoneros have been observed to pair in November and February. Clutches of rather large, white, parchment-covered eggs have been noticed as being laid in September, January, and February. The September eggs were hatched in the following January. The eggs adhere to each other, being covered with a sticky mucus which dries a few minutes after deposition. Eight eggs have been found in a clutch. The young ones will eat each other and, though not nervous when handled, get excited when touched by their brothers and sisters.

### 30. *OXYRHOPUS NEUWIEDII*.

This species so closely resembles the preceding one that the same note will probably apply to both.

### 31. *OXYBELIS ACUMINATUS*.

The local Trinidad names for this slender, sharply-pointed headed serpent is "*Rigoise-Argentee*," "*Liguez*," and "*Whip Snake*." Its length is 1520 mm., of which the tail is 620 mm. The snout is thrice and a half as long as the prominent eye. In colour these snakes are bronzy, greyish, or reddish above, sometimes uniform, whilst others are freckled with brown; usually scattered black dots, or with black edges to some of the scales. There is a black line on each side of the head passing through the eye. The upper lip and lower surface of the head are yellowish white. It is yellowish, pale brownish, or reddish beneath, or it may be speckled or streaked with brown, often with scattered black dots. Sometimes there are two dark brown longitudinal lines. But colour-variation is most difficult to describe. Anyone who has once seen this remarkable looking snake and noticed the long arrow-shaped nose cannot ever mistake it, no matter what the colour may be. The scales are smooth, pitted apically; anal divided; subcaudals paired. The Whip frequents bushes and trees, and greatly resembles a trailing branch. The illusion is made still more deceptive by the snake's peculiar habit of gently swaying its body as the tree branches do in a gentle breeze. Even when caged, where there is no zephyr to influence it, it makes this motion. When the animal is free, it is only when the observer notices the brilliant eyes that he realizes that he is gazing at a beautiful tree-snake. These reptiles feed on lizards and frogs, and when the opportunity offers they may take young birds.



When the Whip is about to capture a lizard, it projects its head towards it. The movement is slower than the minute hand of a watch. At the same time it puts out its long, brown yellow-margined tongue, points together, and holds it stiffly. There is the swaying motion before referred to. Sometimes the tongue is withdrawn and exerted several times, but on these occasions never in the rapid manner of many other ophidians. Just before the decisive moment the tongue stands rigidly upwards at right angles to the snout. A few seconds then elapse, and then there is a sudden lunge forward, and the lizard is caught with inconceivable quickness, usually by the middle of the body. The victim is then passed through the jaws until they close on the head, when the process of swallowing begins. The Whip, except when distended by eggs or after having enjoyed an unusually large dinner, is rarely thicker than an average-sized lead-pencil, while it may be  $4\frac{1}{2}$  feet in length. One under observation laid six large eggs in June. In Venezuela there is a larger closely-allied species which is bright green.

### 32. HOMALOCRANIUM MELANOCEPHALUM.

Total length 500 mm.; tail 100 mm. This is an obscure little snake with smooth unpitted scales, divided anal, and subcaudals in two rows. It is red or pale brown above, with or without three or five more or less dark longitudinal lines. The head and nape are dark brown or black, with the sides of the snout or lip behind the eye yellow. Hinder part of the head with two more or less distinct yellow spots or a yellow cross-bar. Lower parts uniform yellowish white. This reptile is to be found in moist and shady places and deep down in the fallen leaves in bamboo clumps. It is small and inconspicuous, and I know nothing of its habits. Mr. Ulrich once surprised one in the act of swallowing a little centipede.

## THE POISONOUS SNAKES.

### COLUBRIDÆ.

Series C. **Proteroglypha**.—Poisonous, the poison being conveyed mainly through the anterior maxillary teeth, which are so folded as to appear hollow or perforated.

### The ELAPINÆ.

### 33. ELAPS CORALLINUS.

The local names for the first of the really dangerously poisonous snakes on the list are "Coral Snake" (male), "Serpent-Corail," and "Corail." *Elaps corallinus* is but a small creature, and is only likely to do harm if trodden upon by a bare-footed person or is roughly handled. Its fangs are comparatively small, and cannot penetrate thick leather or clothing effectively enough to

make a wound. The length is 790 mm., of which 70 mm. belong to the tail. In the British Museum Catalogue the description is as follows:—

“Eye measuring two-thirds to three-fourths its distance from the mouth in the adult. Rostral broader than deep; frontal a little broader than the supraocular, once and a half to twice as long as broad, as long as its distance from the end of the snout, a little shorter than the parietals; latter as long as their distance from the internasals; one præ- and two (rarely one) postoculars; temporals 1+1, the anterior sometimes fused with the sixth labial; six upper labials, third as large, or a little larger than the fourth, third and fourth entering the eye, three or four lower labials in contact with the anterior chin-shields, which are shorter than the posterior. Scales in fifteen rows. Ventrals 179–231; anal divided; subcaudals 30–47. Body with black annuli edged with yellow, separated by red interspaces which may be more or less profusely spotted with black; head black above temples, and often a more or less broad band behind or partly on the parietals, yellow.”

This is a good description, but in my observation, which covers a long series of individual specimens, the edges described above as yellow are white. The black rings with their white edges are generally only about half the width of the black-spotted red bands. The scales are smooth, without pits. The subcaudals are in two rows or partly single, partly in two rows. The fangs are two on each side of the upper jaw and are in front of the other teeth.

Here it would be as well to remark on the word “Coral” that the writer has been informed that as applied to this snake and the next, “Coral” is the corruption of the Spanish word “Corro,” meaning a ring. This is a good description of these creatures, which are girdled with red, black, and white rings. When referring to the colour of a snake—that is, a coral-tinted serpent: a young *Oxyrhopus coronatus*, for instance,—the South American Spaniards say “Corallile.” The Trinidad peasant, who loves to clip his words as much as possible, with much ease abbreviates this to “Coral,” imagining that the red is the distinctive marking, and not the *rings*, and thus in referring to these ringed venomous serpents the significance of a most expressive descriptive word is lost. Moreover, the country people of the colony consider that the difference in the arrangement of the colours of this and the next species indicates the sexes, the present one being the “male.” *E. corallinus*, however, is a smaller animal, and its colour-pattern is more regular in arrangement than that of its cousin.

In captivity it also differs in its habits, for although not averse to feeding in the daytime, it is most lively at night. It is fond of water, and one which was for some time under observation bathed regularly every day. If the bath was not changed frequently, it neglected its diurnal dip. In the Cerro Oropouche

Mr. Urich once saw a Coral bathing in a small pool by the roadside. So far as has been observed, the Corals of both species are snake-eaters, and this particular Elaps has been seen many times devouring little ground-snakes (*Atractus trilineatus*), which rarely exceed twelve inches in length. These snakes it attacks and swallows at any time of the day or night. A ground-snake four inches long was introduced into the Coral's cage at 9.14 p.m. and had been swallowed by 9.25 p.m. One, nine inches long, was seized and entirely engulfed in thirty-nine minutes. The actual process only occupied six and a half minutes. The little victims fought bravely for their lives, twisting their bodies round the destroyer's head into wonderful knots, and doing everything in their power to stay the gorging process. Their tails twitched and wriggled as they disappeared, which would seem to indicate that the venom of this Elaps is not so potent as that of the next one to be noticed. *Elaps corallinus* has been observed to pair in January. Two eggs were found with one in July.

#### 34. ELAPS MARCGRAVII.

Local name: "Coral Snake" (female). "Corail." Total length 1120 mm.; tail 100 mm. In the 'Catalogue of the Snakes in the British Museum' the species is described in the following terms:—

"Eye measuring two-fifths to three-fifths its distance from the mouth. Rostral broader than deep; frontal as broad as or broader than the supraocular. once and a half to twice as long as broad, as long as its distance from the end of the snout, shorter than the parietals; latter a little longer than their distance from the internasals; one præ- and two postoculars; temporals 1 + 1, anterior usually much longer than the second; seven upper labials, third much larger than fourth, third and fourth entering the eye; four lower labials in contact with the anterior chin-shields, which are as long as or a little shorter than the posterior. Scales in 15 rows. Ventrals 210 240; anal divided; subcaudals 23-42. Body with black annuli disposed in threes, the middle one usually wider; six to ten sets of annuli, separated by broad red interspaces, which, like the narrow greenish-white annuli within each set, may be dotted or the scales edged with black; snout yellow, the end usually black; a more or less black band across the middle of the head; back of head red, the upper head-shields sometimes all black, edged with yellow."

To this may be added:—"Scales smooth, without pits . . . subcaudals in two rows or partly single, partly in two rows."

Like the preceding species this Coral is a nocturnal animal, and is at night very lively and quick in its movements. In daylight it is sluggish and loth to bite, and usually allows itself to be handled to almost any extent. Of this snake the late Count de Verteuil wrote:—"It can be handled without danger, children very often playing with this viper (*sic*), encircling it round the

neck. I have myself more than once carried about Corals, not suspecting they were venomous. The apparent innocuity of the Coral arises from the peculiar conformation of its head and mouth; the head is of the same growth with the body, and not separated with a distinct neck; nor can it on account of its anatomical organization open its jaws sufficiently to seize and bite any bulky body. It is nevertheless highly poisonous." All of this is perfectly true, but it is not always safe to handle a Coral. Some years ago a drunken East Indian at Couva was going about the village playing with a Coral snake and carrying it in his bosom. At last the snake could bear no more and bit its tormentor, who died some hours afterwards. De Verteuil says that casualties through the bites of Corals are rare. In his work on Trinidad, however, he relates one instance. Two robust African labourers were at work in a cane-field on La Marguerite Estate, in the ward of St. Joseph. Having discovered a Coral, by way of amusement they laid hold of it. Of their fellow-workers' warnings they took no notice, but, on the contrary, continued to tease the reptile, and even put its head in their mouths. Eventually they were both bitten, one on the lip and the other on the tongue. This happened about 1 p.m. The one who had apparently most irritated the creature soon began to reel about as if drunk. Convulsions followed, and he was dead about eight o'clock; the other died an hour later. This Coral was preserved by Dr. Court. It measured four and a half feet long, and the writer saw it in the Court Collection at the Victoria Institute, which was afterwards destroyed by fire. It was distinctly referable to the species under consideration. The Hon. Albert Carr relates a more recent incident. At Brasso Caparo a fine black man, heavily loaded with cacao, stepped into a drain and then on to the road. In the drain, he trod on and was bitten by a Coral. The injury was on the thin skin between the toes. Mr. Carr did not see the victim until many hours after the occurrence, when remedies were too late to be of any use. The man died the next morning. Some years ago, late one evening there was great excitement in Queen Street, Port of Spain, for a large Coral snake of this species was crossing the road, and was obviously attempting to get into Trinity Cathedral enclosure. I happened to be at my office that evening, and I was called and with a stick I went out to catch it. The night was dark and the street lights were distant. There was a crowd of about one hundred agitated people. A friendly shoemaker held a flickering candle. Whenever an attempt was made to hold down the snake with the stick the reptile turned and bit it, and its poison fangs could be heard grating on the wood. It was taken at last. It was 42 inches long. Undoubtedly this snake would have bitten and probably killed anyone who had taken it up. The largest Coral I have seen was 46 inches long. These snakes are often found on sugar estates, hiding under the leaves on the ground, but they prefer damp ravines, and cacao estates where there is

shade, for they are thirsty animals. So far as we know, this *Elaps*, like the preceding one, is a snake-eater, though Mr. Urich knows of an instance where a *Scolecosaur* lizard was a victim, and Mr. R. L. Ditmars, an American ophiologist, has informed me that he has known it to destroy and devour skink-like lizards. My personal experience is that it is always difficult to get them to feed. When they have done so, their prey has always been small harmless snakes. There has never been an opportunity to try them with young *Lachesis*. It would be interesting to know the result when such highly venomous snakes are introduced to each other. Probably both would die of snake poison. Wounded Coral snakes often disgorge ground snakes. For a snake *Elaps marcgravii* is possessed of a comparatively small solid head and four short fixed fangs, two on each side, which are situated rather further back than the long folding teeth of the vipers. The fangs in each pair are side by side instead of following each other. I do not know whether both fangs in a pair are poison conductors, though both have grooves. The shortness of the fangs and the small size of the mouth prevent these snakes from biting anything large. This *Elaps* relies considerably on its poison to overcome its victims. To one specimen, 33 inches long, a *Liophis melanotus* was introduced. It had disappeared the next day, and there was a slight increase in the Coral's circumference. A week later a young *Drymobius boddaerti* similarly vanished. Three days later another *L. melanotus* was disposed of. All these snakes manifested the greatest uneasiness, nay terror, in the presence of the Coral, though as long as daylight lasted the *Elaps* paid them no attention. Fifteen days later, at night, a *L. melanotus*, of 17½ inches, was put into the cage. The moment it entered, the Coral raised its head, but immediately resumed its quiescent attitude. Subsequently it bit the visitor near the tail. The poor victim was at once released, and actively moved about with the tail raised. In five minutes it laid its head down slightly on one side; its body twitched as if in pain, and three minutes later it was dead. The Coral at once seized it four inches from the head, then worked it through its jaws to within an inch of its head; then let go, and seizing it again, worked down the body for about three-quarters of its length. It let go again, and then caught hold of the dead snake within an inch of its head, worked it to the muzzle, which it got into its mouth, and then proceeded to swallow it by sidelong jerks, first right, then left, in rapid succession. After it had swallowed about half the dead snake, it began to make the usual drawing, muscular motions which are characteristic of the deglutition of most of the Ophidia. After the meal the Coral yawned several times. During the first part of the swallowing the victim was held down by a bite of the Coral's body, from 2½ to 3 inches from where its jaws were working. The swallowed snake was nearly as thick as the Coral, and when it was going through the preliminary of being passed through the latter's jaws, there were little crackling noises, as if the bones

were being broken. The whole operation of killing and gorging lasted one hour. In consequence of being frightened, the Coral vomited its meal during the night. These observations, with some variations, were repeated several times. The victims usually died in four or five minutes. One was bitten three times in rapid succession. One was held until it was dead. In order to ascertain the effect of the bite of this Elaps on a warm-blooded animal, Mr. Ulrich, who helped me on all these occasions, shaved the thigh of a large well-grown rat. The Coral was forced to bite it at 8.3 P.M. The rat immediately got drowsy. Subsequently it began to pant violently, but was still drowsy. Then the tail began to twitch, as also did the muscles in the region of the spine. At 8.11 P.M. convulsions began. At 8.14 P.M. the heart had ceased to beat. Eleven minutes elapsed from bite until death. When biting, the Coral held on for about 15 seconds.

#### “VIPERIDÆ.

“Facial bones movable; . . . maxillary much abbreviated, erectile perpendicularly . . . supporting a pair of large poison fangs without external groove . . . Poisonous.”

“Subfamily CROTALINÆ. The ‘Pit-Vipers.’ So called because there is a deep cavity or pit between the eye and the nose lodged in the hollowed-out maxillary bone. This pit is lined with a modified continuation of the epidermis, and is amply supplied with branches from the trigeminal nerve. It is undoubtedly sensory, but we do not know its function.”—Dr. H. Gadow’s ‘Amphibia and Reptiles.’ The Cambridge Natural History.

#### 35. LACHESIS MUTUS.

Local Trinidad name: “Mauppire Z’Ananna,” Pine-apple Mauppire. British Guiana name: “Bushmaster.” Total length 1995 mm., tail 170 mm. This snake is thus described by Dr. Boulenger in the ‘Catalogue of the Snakes in the British Museum’ :—

“Rostral as deep as broad or a little broader than deep; nasal divided; upper head-scales very small, granular, smooth or obtusely keeled; supraocular narrow; two or three scales separating the internasals in front; 10 to 15 scales on a line between the supraoculars; four or five series of scales between the eye and the upper labials; temporal scales obtusely keeled; 9 or 10 upper labials, second usually forming the anterior border of the loreal pit, third very large. Scales tubercularly keeled, feebly imbricate, in 35 or 37 rows. Ventrals 200–230; anal entire; subcaudals 32–50, all or greater part in pairs and followed by very small keeled scales covering the end of the tail. Yellowish or pinkish above, with a series of large rhomboidal

dark brown or black spots enclosing smaller light spots; a black streak from the eye to the angle of the mouth."

This snake, which is the largest venomous reptile found in either North or South America, is indigenous to Trinidad. De Verteuil mentions one killed at Couva which measured eleven feet. Seven- and eight-foot Mapepire are not uncommon. The reptile is often found in burrows occupied by Iappe (*Cælogenys paca*), and sometimes in the holes in which the Tatou (Armadillo—*T. novæmcincta*) resides. My first acquaintance with the wild Mapepire was in this wise. When walking in the High Woods of Caparo with Mr. Albert Carr and his brother, the late Mr. Artie Carr, we heard a dog yelping and a man calling for help. We crossed a deep ravine, and on the opposite bank we found a Peon, who said that his dog had been bitten by a Mapepire. The wound was in the animal's shoulder, and Artie Carr cut the punctures so that the blood would flow readily, and he heroically tried suction. He also forced the dog to swallow a local remedy which is known as "Melidor's Cure for Snake-Bite." The animal was a small one, and it was very thin and in bad condition. In spite of all that was done for it, three-quarters of an hour after it was bitten it died. We proceeded to open the burrow in which the snake was said to be. After a lot of digging, for perhaps half an hour, during which a great quantity of earth was removed, the Mapepire was found four or five feet in, and we took it alive. It was quite a small snake, only being about  $5\frac{1}{2}$  feet long. It was very quiet until it was actually touched, and even then it did not make much resistance. The next one I met was beyond Tabaquite, soon after the railway was opened in that district. We had been one or two days in the forest, and had reached a spot where we could distinctly hear the sea beating on the eastern coast. While at "coffee" early in the morning, we heard a troop of Red Howlers engaged in their orisons. The noise was appalling. As they were close at hand, we set out to try to shoot one. We had not gone more than a few yards when the breaking, and fall, of rotten branches warned us that we were near the monkeys. At the same moment one of the men called out "Serpent!" Looking down, I saw almost at my feet, in loose coils, one of the largest Mapepires I have ever seen. It was nine feet long. Mr. Arthur Carr promptly cut a forked stick, which I planted astride the snake's neck, pinning it to the ground. Holding the stick firmly, I looked up and saw a troop of eight or nine Red Howlers pass in procession, in single file, high up in the trees—it was a sight I shall never forget. The party loosed off a good many guns, and killed three young females before the rest of the troop escaped. The game was collected, after which we proceeded to put the snake in a bag. During the whole of those exciting moments, while five or six men ran and shouted, whilst at least three were shooting with double-barrelled guns, that snake never moved. It might have been dead, it was so still. It only began to squirm and wriggle

when it felt a warm hand on its neck, and then it opened its gaping jaws widely and moved down and displayed its inch long, cruel, formidable fangs. Mr. Emmanuel Pereira, who caught a Maepire at Guapo, assures me that he carried it in an open box for a distance of 150 feet. He kept the creature a fortnight, during which time it devoured a wood-rat. Some mischievous person wounded this snake during its journey to town, and it was just dead when it reached me. It measured 91 inches. But Maepire Z'Ananna is not always so docile as these instances would seem to indicate. Sometimes it is roused to the greatest fury, and then it strikes out rapidly and repeatedly at its enemies. One such occasion Mr. Artie Carr told me of, when all the dogs were baying round the angry reptile, which, however, fortunately did not succeed in biting any one of them. Mr. Albert Carr relates how one Maepire (7 ft. 10 in. long and 3 in. in diameter in the thickest part) was dragged by a dog out of a hollow balata-tree before it woke up. Half-a-dozen dogs attacked it, and four were promptly bitten. The first died almost immediately and the second succumbed within a quarter of an hour. The others were caught and attended to, and recovered in a few days. The remedy used was one locally known as "Melidor's," and is described as composed of certain roots, barks, and seeds in rum. It is said to be "a pleasant though strong balsamic bitter." Maepires have their natural enemies in the forests, for, in a bit of High Woods at Mr. Rorer's estate at Guaiaco, I found the freshly-killed remains of a very large one. The head and first half of it had been devoured.

I have had to do with many Maepires in confinement, and my experience is that they are most timid and retiring creatures. They are extremely difficult to manage, because, as a rule, they absolutely refused to feed. I have tried them with eggs, mice, rats of all sizes, little rabbits, chicken, lizards, frogs, and any other small animal I could get, both alive and dead, but with very little success. Maepires kept out of doors in a wire-net-bottomed box sunk in the earth, with two or three feet space above, furnished with a hollow log to lie in, and the top covered with a wire net, have twice or thrice killed and devoured half-grown common rats. Subsequently they have either disgorged the meal or have died when sloughing—always a difficult operation with these snakes in captivity. As a rule the snake will even allow the rats to bite it, and will only try to escape, although it must know that one tiny prick of its terrible fangs would mean speedy death to the tormentor and peace to itself. But it does not even attempt to bite. One, which I obtained at the end of December 1915, refused all the animals enumerated above, and actually amicably shared with a Manicou Gros Yeux (*Didelphys philander*—an opossum, about the size of an average rat) a small box which was in its cage. The Manicou was apparently very frightened at first, but the snake did not show any hostility to his room-



mate. I have learned by experience that when a Maepire in confinement shows viciousness it is a sure augury of its speedily approaching death, which occurs a day or two afterwards. Numbers of Maepires only survive capture six weeks or two months. Four months is the longest time I have had an adult in captivity. Besides being a very timid animal, which starves itself to death, there is another reason why they are so short-lived. The Maepire's backbone is not so flexible as is the spine in most other snakes. When one takes a Maepire in his hand, he naturally holds the neck very tightly, and in such a way that the enclosing fingers cannot be punctured by the long mobile fangs, which can be used independently of each other—one may be closed or partly closed and the other may be fully open; it is dangerous to put the fingers right round the neck. In the mean time the snake is twisting, wriggling, and squirming, and it is not very long before the operator hears a little sharp sound as if something had snapped. The snake has injured its backbone, and sooner or later the hurt is certain to prove fatal. On one of the few occasions when I have had two Maepires together I wished to transfer them to bags. I heard the snap with the first, but got it into the bag safely. When the second was taken up, there was also a snap. The animal relaxed with open jaws, and lay dead in my hand. The first snake died three or four days later. Since then I have never touched a Maepire, and I have impressed on all those who catch them that they must do so without handling them in any way. Whenever it is necessary to transfer a Maepire from a bag to a cage, or *vice versa*, it is best to allow the snake to perform the operation itself. It may be regarded as surprising, but nevertheless it is true, that Maepires, like all other snakes, when they know what is required of them, having been once put through the routine, never forget it, and are willing to do what one wants them to do. All that is necessary is a little patience.

One October, some years ago, Mr. Arthur Carr brought me a very small Maepire Z'Ananna in a cigar box. It was a foot or fifteen inches long. There was another where it was found, but the men killed it before Carr saw it. Whereas the young of the other Maepire (*L. atrox*) is often brought to me, this was the smallest living young Maepire Z'Ananna I recollect having ever seen. At first it was very shy about feeding, but eventually devoured mice regularly. It, like the adults, was sometimes very adverse to feeding, and on one occasion a mouse which was allowed to stay rather too long in the cage nipped off the end of the snake's tail, and with it, of course, the nail like scale which is such a marked characteristic of the species. Like the adults this little snake had much trouble at the sloughing periods. On the first occasion he did not shed at all and the old skin remained on. When his eyes turned blue again—a certain indication of the approach of the sloughing period—I put him into a bottle of water, and allowed him to soak for many hours, after which both

sloughs were successfully removed by hand, a very delicate and risky operation, although the little chap was quite quiet during the process. On another occasion, when the blue stage had passed off, he was put in a wide-mouthed bottle of water and kept in by a piece of mosquito curtain. His confinement lasted five days. When the netting was removed he left the bottle, and a perfect slough remained in the water. On the next occasion, three months later, he shed his skin naturally without any help, and the slough was nearly perfect—the only time that a Mapepire Z'Ananna in my cages has performed this very necessary function satisfactorily. At first, when feeding he was very ready to abandon his meal, but he gradually became bolder and ultimately did not mind being watched. He even condescended to devour dead mice, and when I approached his cage he would lift his head expectantly. His victims expired very quickly, and his methods were precisely those of the rattlesnake. He met the fate of all pets. I was away from home for a few days and he was fed too frequently. The day I returned he was obviously unwell, in pain, and he was moving about with his mouth open. During the night he died of intestinal obstruction, a trouble to which all captive snakes are subject unless there is plenty of variety in their food. This interesting Mapepire, which had lived sixteen months in a cage, measured  $45\frac{1}{2}$  inches long.

Mr. Arthur Carr used to relate a singular encounter with a Mapepire Z'Ananna. Some East Indians were out on a nocturnal hunting exhibition, and one of them carried a light. They halted for a moment, when they were suddenly horrified at seeing slowly rising out of the undergrowth the great head and flickering tongue of an enormous Mapepire which was approaching the lantern. A Creole who was there dexterously beheaded the creature before it had satisfied its curiosity. Next morning the head was found with the fangs extended and the jaws closed on the stem of a young tree. The Mapepire agitates its tail when excited, and rapidly striking the leaves or ground, makes a noise not unlike the rattlesnake.

The viperine snakes are ovoviviparous—that is to say, the young are developed in eggs which are hatched on, or immediately before, exclusion from the body. There are some exceptions, but up to July 1903 I was of the opinion that all the *Lachesis*, in Trinidad at any rate, produced their young alive. Mapepire Balsin (*L. atrox*) had done so repeatedly I knew, and so also had the St. Lucia Fer de Lance (*L. lanceolatus*), and I supposed that Mapepire Z'Ananna followed that rule. Was it not recorded in the 'Journal of the Trinidad Field Naturalists' Club' that the Secretary exhibited (Nov. 1894) two young Mapepires (*Lachesis mutus*) which were taken from their mother by Mr. H. Hutton at Pool. There were a great many more, probably forty. By reading I had learned that the rattlesnake, which Mapepire Z'Ananna so closely resembles, gave birth to living young, and therefore I had no doubt about the breeding-habits of the species

under review. The Messrs. Carr (without contradicting this view in terms) seemed to be doubtful on the point. One day Arthur Carr forwarded me an immense Mapepire Z'Ananna. I was away at the time, and the animal was placed in a cage. I returned, and on going to see the new snake, found that she had laid ten or twelve eggs, larger than those of a duck. The snake was coiled round some of the eggs, and there were others under her folds. The cage was a small one. The eggs were soft, white, and covered with a parchment-like envelope. There was not too much room for the snake, but she looked as if she was trying to incubate them. As the eggs seemed to be shrivelling, they were placed in an incubator. There they dried up entirely. The 'Field' published an account of the occurrence, whereupon Dr. Boulenger, of the British Museum, wrote as follows in a subsequent issue of the same paper: -

"The record of an oviparous viperine snake, *Lachesis mutus*, in the 'Field' of August 8th, is a very important addition to our knowledge. Mr. R. R. Mole, to whom this discovery is due, has sent a photograph of the snake with its eggs. The scale of reduction will be realized from Mr. Mole's statement that the eggs are larger than a duck's. The mother is about 7 ft. 6 in. in length. The photograph was taken by Mr. C. S. Rogers, of Port of Spain, Trinidad. Until 1895 all viperine snakes were believed to be ovoviviparous. In that year Dr. Günther mentioned the exception offered by the African *Atractaspis*, a statement since repeated in Gadow's Reptile volume of the Cambridge Natural History. Dr. Günther's information was derived from eggs of *Atractaspis irregularis* from Uganda, collected by Mr. Baxter in 1893. These eggs, preserved in spirit in the British Museum of Natural History, are 2 in. long. It has since been observed at the Zoological Gardens that another African viper, *Causus rhombeatus*, is oviparous. That the two modes of parturition should occur in the same family, or even in the same genus of reptiles, is not very surprising from what we know of our two species of *Lacerta* and of the different species of *Tropidonotus*, the type of which is our common grass snake, and is oviparous, whilst some American species are ovoviviparous. I may add that *Lachesis mutus* is among the snakes reported to shelter their young by swallowing them. A well-known mining expert in British Guiana is stated by Mr. Quelch to have observed one of these snakes to give out from its mouth, after being severely wounded, a number of small specimens. Incubation of the eggs by the mother has hitherto only been observed in pythons." (Sgd.) G. A. Boulenger.

Some years later the following references to this occurrence appeared in the 'Field':—

"Among the illustrations to the Report of the American Museum of Natural History for the year 1910 is a photograph of a model of a 'bushmaster' snake (*Lachesis muta*) and its eggs recently added to the exhibition series in that institution. The

legend to the illustration states that the species is 'one of the largest and most venomous of poisonous snakes of the New World, and supposed to be the only species of crotaline snakes that lays eggs.' The compiler of the report has evidently overlooked the article in the 'Field' of Jan. 1, 1910, by Mr. R. C. Leigh on 'An Oviparous Indian Viper,' in which it is shown that the Himalayan Mountain Viper likewise lays eggs. In that article the Mountain Viper is called *Trimeresurus monticola* (Günther). But in Mr. Boulenger's 'Catalogue of Snakes in the British Museum' it is referred to the same genus as the Bushmaster under the name of *Lachesis monticola*. Although this is not definitely stated, Mr. Leigh appears to have been under the impression that his discovery was the first record of the oviparous habit among the Crotalinae, or pit vipers. He had, however, been anticipated by Mr. R. L. Ditmars, who, in the American edition of his 'Reptiles of the World,' published in 1907 adduced evidence that the Bushmaster lays eggs. This information was supplied by Mr. R. R. Mole, of Port of Spain, Trinidad, who wrote Mr. Ditmars as follows:—

"I believe the *Lachesis* which I hope you received safely contains eggs. You will remember that one I had laid a batch of ten or twelve eggs three years ago. I have since learned that similar bunches of eggs have been occasionally found by hunters in holes inhabited by the Paca (*Calogenys*) and the Armadillo and other burrowing animals in which specimens of *Lachesis mutus* are often found. I have seen these snakes dug out of such holes, but I have only seen the eggs laid in my cage."

But the foregoing discovery as to Mapepire Z'Ananna has not been allowed to go unchallenged. In December 1915, Professor C. R. Halter, of the Department of Herpetology, American Museum of Natural History, wrote to me to the effect that Dr. Vital Brazil had informed him that he had hundreds of female Bushmasters (Mapepire Z'Ananna—*L. muta*) in his keeping, and without exception they gave birth to fully developed living young: none laid eggs, and he asked me for my experiences. I wrote to him, narrating the above. I also wrote to the Hon. Albert Carr on the subject, and he replied as follows:—

"Caparo, 6th February, 1918.

"With reference to our conversation on Friday last on the subject of the manner in which the Mapepire Z'Ananna (*Lachesis muta*) bring forth their young, I may say that both Artie and I were of the strong opinion that they laid their eggs in burrows in the ground, and that we had on many occasions come across quite a number of eggs (clearly snakes' eggs) in lappe holes especially, and tatous' holes occasionally. Our belief that these eggs, always of the same kind, and similar in every respect to the lot you showed us many years ago in a cage with a live Mapepire which you told us had laid them, were Mapepire's eggs had been strengthened by the assurance of Old Boney (a Spanish Peon), that calm and experienced hunter of upwards of 45 years

in these parts. Any doubt I may have had vanished when I saw the eggs in your cage. There can be no fear that such creatures as Iguanas and Mattas lay such eggs, as their eggs are too well known, while none of the colubrine snakes lay eggs in any way approaching in appearance those found by us in the forests, and by you in your cage. If the above is of any use to you, you are at liberty to make use of it and to mention my name." (Sgd.) A. B. Carr.

Mr. Reginald Carr supplemented this with the following:—He had found similar eggs many times. There were never more than ten or twelve. He had known six and had seen two and three, and once only one. Sometimes the eggs looked as if some animal had been feeding on them. There was no doubt in his mind that these eggs were not those of Cribos or other large harmless snakes. The Spaniards who hunt in the Trinidad woods all say that Maepire Z'Ananna lays eggs.

There the matter rests for the present. I am loth to oppose my opinion to the statement of such a distinguished herpetologist as Dr. Vital Brazil, but there is no doubt that the eggs were laid in my cage. In his book, 'La Defense contre L'Ophidisme,' Dr. Brazil says *Lachesis muta* is a rare snake. I agree with him. I think one of the reasons it is so rare is that it is not nearly so prolific as the much commoner *L. atrox*, which sometimes has as many as sixty young ones at a time. It is a very interesting point and I should like to see it definitely settled, but potential mothers of *L. mutus* are very rare indeed.

A coherent and reliable story of a case of snake-bite is also very rare, and therefore I was glad to get the narrative of the Hon. Albert B. Carr, who had a terrible experience with a Maepire Z'Ananna. He was a young fellow at the time, and was then, as he is now, a man of indomitable pluck and determination. He tells the story very graphically, and there is no doubt that he owes his life to his resolve not to succumb to the potent poison of a "mere creeping thing like a snake." I have no doubt that a person cast in a less resolute mould would not have survived the night. Here is Mr. Carr's description:—

"I have yours of the 18th February asking me to give my experience of the bite of the Maepire Z'Ananna, which I received in the late 'eighties whilst pioneering the almost unknown forests of Caparo. At the time of the occurrence, to the best of my recollection in the year 1889, I took full notes, which I intended to publish—this, however, for one reason or another, I have not done. On receiving your letter I looked for the paper, but I have misplaced it. I, however, retained a vivid recollection of that never-to-be-forgotten incident—the most tragic of my life. Here is the story.

"Whilst Lappe hunting on the low hill-ranges which line the Mamural Valley, accompanied by my brother Reggie and a faithful friend and servant, Sammy, we started a Lappe which sought cover in a hole on the slope of a thinly-wooded hill. We

set to work in the usual way, with cutlass and spade, to dig out the quarry. In about an hour it was stabbed, and withdrawn from the burrow. Noticing that the end of the hole had not been reached, and knowing that it often happened that there was another Lappe, or an Armadillo, in the same hole, which was there before the entry of the one we had pursued, I inserted a thin and pliant rod, and at once touched some living creature three or four feet further in. To find out what it was, I thrust in my hunting-knife and arm as far as I could reach, and moved it gently up and down and felt what I thought was the scaly hind-quarters of an Armadillo. I noticed no movement but a light kick to the blade. I paid no attention to it, and never for a moment suspected the presence of a snake, as I had on many occasions noticed a similar movement and had afterwards taken a Lappe or Armadillo, but never seen a snake, although I had been hunting for many years. In later years, however, I found Mapepire ZAnanna occasionally in both Lappe and Armadillo holes, but principally in the former. If I had had any doubt, it would have been soon laid to rest, for Sammy called out 'I hear it, Sir! it's a Lappe, let me probe the hole.' Probing means finding out the direction before digging is undertaken, and I again inserted my hunting-knife and was immediately bitten on the inner side of my left thumb. As I withdrew my hand, I saw the head of a large Mapepire ZAnanna holding on to my thumb. It was only for the fraction of a second, and then the snake let go and withdrew into the burrow. As quick as thought I called my brother to open my haversack and take out my penknife and a phial of 'Mehdor's Antidote to Snake-Bite.' At the same time I gripped my wrist with all the power of my right hand, and I called to Sammy to cut a long pendant root of *Philodendron* (Seguin) with which to make a ligature. But these orders given, imagine my dismay when the penknife was nowhere to be found, and the antidote on which I pinned my faith (as it had to my knowledge been used with success in more than one case where dogs had been bitten) had been reduced to one half-dose by leakage through a faulty cork. Failing the penknife, my brother used his hunting-knife, which had been blunted during the progress of the day. After sawing across the punctures (it could not be called cutting) in two directions, a little of the antidote was applied, and I drank the rest. Sammy, meanwhile, had applied the ligature. The whole of the treatment did not occupy more than three or four minutes.

"The first sensation experienced was that of a sharp stab. Then followed intense pain, accompanied by a feeling of cold, attended by shivering and giddiness. The last two sensations disappeared on my taking a draught of the antidote, which I presume was due to there being alcohol in it. The thumb and hand became much inflamed, and the forearm and wrist were extremely painful. The dressing of the wound over, the next best thing to be done was to hurry home as quickly as possible,

and as there was but an hour of daylight before nightfall, and a distance of three miles to traverse through the forest with all its natural impedimenta of lianes and thorny vines, there was none too much time. Some loose earth was thrown into the hole, which should have been tightly rammed. The trees were blazed round it. Then we set off, I leading as the others were not sure of the way. The Lappe was shouldered by Sammy, and I carried a large Agouti, which, being hung as a sling, afforded a soft and partially warm support for my very sore and fast-swelling hand and arm. After a rapid tramp for an hour, during which we picked up a large Morcois (tortoise), home was reached—not the well-found home where stimulants and a medical chest exist—simply a large, airy, thatched ajoupa, containing none of the accompaniments of modern civilization. The excitement of walking over, a quarter of an hour later my terrible troubles began. My hand had begun to take the shape, and threatened to assume the dimensions, of a three-quarter-sized football, which it actually did towards midnight. My sufferings throughout the night and in the early hours of next morning were most intense, and it is difficult to say in which part of my body the pain was most acute—at the wound, in the armpit, the heart, or the abdomen. I am inclined to think the last-named was where the pain seemed to be a death-racking cramp.

“At 8 P.M., being unable any longer to bear the pain caused by the ligature at the wrist, I had another placed over the elbow, and then removed the first one. I then took to my bed, and an hour later a fit of vomiting came on, which continued at frequent intervals until 1 A.M. The vomit was mainly black, and I thought it consisted of congealed blood from the lungs. This, added to the great pain I had undergone for so many hours, did not tend to make matters any better for me, but rather resulted in completely prostrating me, and it was not until 7 A.M. next day that I was somewhat revived after taking a few sips of black coffee—the first food of any kind to pass my lips since noon on the previous day. From that time until five weeks later I was unfit for all work. The thumb, meanwhile, had undergone a great change, for practically all the flesh and the nail fell off. The new flesh grew slowly, and when quite healed over, the thumb was only about three-quarters of its original size, while for years it was perfectly numb. There was no treatment beyond that administered in the woods. My brother sat up all night with me, and measured my arm at intervals of fifteen minutes and made notes thereof. These showed that the swelling increased until 1 A.M., and then began to decline and by daybreak had very considerably decreased, as also had the pain.

“Within a fortnight of the bite, my brother Artie, proceeding on the description of the hill and the environment which I gave him, succeeded in finding the hole, and to his and my disappointment found that the snake had made its escape through the loosely-packed earth which had been hurriedly thrown into it.

His mission, however, was not altogether a failure, as he found the freshly-cast skin of a large Mapepire Z'Ananna within a few feet of the hole where I was bitten. A few persons, all townspeople, and among them Mr. J. H. Hart, Superintendent of the Botanic Gardens and botanist, questioned my statement that I had been bitten by a Mapepire Z'Ananna. Mr. Hart claimed that as the snake had escaped, no reliance could be placed on my narrative. All Trinidad woodsmen know positively, and their knowledge of woodcraft is quite sufficient for me, that none of our venomous snakes but the Mapepire Z'Ananna lives in the burrows of Lappe and Armadillo, and that the only other large poisonous ophidian of the island, viz. the Mapepire Barcin, or Trinidad Fer de Lance, inhabits the banks of muddy streams, such as the Caparo and the Cumuto.

"Very few people lived in Caparo in those days, but the news spread, and the very next day the only woman within miles came to see me, and to warn me that if before I was well I met an expectant human mother I would surely die. I laughed, and feeling stronger the next day, made the journey to town, when I met not one, but many, and yet I am still, 27 years later, alive to tell the tale." (Sgd.) A. B. Carr.

Mr. C. S. Rogers, the Forestry Officer, tells me that a dog, which was in good condition, was brought to him in a moribund state. It had been trying to get into a hole, when it was bitten on the top of the head by a snake—presumably a Mapepire Z'Ananna. The two punctures were plainly visible, and the head was swollen. Mr. Rogers opened the wound, taking care not to injure the thin skin enveloping the skull, and rubbed in as much permanganate of potassium as would cover a threepenny bit. The dog recovered in the course of a week. Mapepire Z'Ananna are found in various parts of the country, but are said to be most common in the northern ranges, where they are frequently found in the neighbourhood of quarries and amongst rocks.

### 36. *LACHESIS ATROX* L.

Local Trinidad names: Mapepire Balsain, M. Barcin, M. Valsin, Fer de Lance. The young ones are called Rabo Frito. Total length 1110 mm.; tail 180 mm. The following description of this snake appears in the 'Catalogue of the Snakes in the British Museum':—

"Snout obtusely pointed, with sharp, slightly raised canthus. Rostral as deep as broad, or a little deeper than broad; nasal divided; upper head-scales small, imbricate, more or less strongly keeled, in 5 to 9 longitudinal series between the supraoculars, which are large; a pair of large internasals forming a suture with each other, and a large canthal; two postoculars and one, two, or three suboculars, separated from the labials by one series of scales; temporal scales keeled; seven (rarely eight) upper labials, second forming the interior border of the loreal pit. Scales in 25 to 29 rows, strongly keeled, the keels on the posterior part of the back



very high, swollen in the middle and much shorter than the scale. Ventrals 161-216; anal entire; subcaudals 47-73 pairs. Brown above, with more or less distinct dark, light-edged cross-bands or triangles with the apices approximating on the vertebral line; a more or less dark streak from the eye to the angle of the mouth; belly yellowish white, much speckled and blotched with brown, or brown spotted with yellowish white."

In the 'Catalogue of Snakes in the British Museum' *Lachesis atrox* appears as the third species of the genus *Lachesis*. No. 1 is *L. mutus*; No. 2, *L. lanceolatus*, which is indigenous to South America, and is found in all the countries from Mexico in the North to Brazil in the South and Peru in the West, and also in the West Indian Islands of St. Lucia and Martinique. No. 3, *L. atrox*. Now, while there is no chance of anyone confusing *L. mutus* with either *L. lanceolatus* or *L. atrox*, the difficulty of distinguishing between the last two snakes is very great indeed, for they are the Tweedledum and Tweedledee of the Ophidia. Indeed, after describing *L. lanceolatus*, the distinguished author of the Catalogue, Dr. Boulenger, says:—"This species may have to be united with the following (*L. atrox*). The only character by which I have distinguished the two, viz. the length of the keel on the dorsal scales, is not dependent on age or sex, as had been supposed. Some specimens of *L. lanceolatus*, however, approach *L. atrox* in the swelling of the scales at the base of the keels, and are thus intermediate between the two supposed species. It is also not impossible that two or three species are confounded here under *L. lanceolatus*, but I have been unable to trace any limits or to find any correlation between the modification in scaling and coloration." Dr. Brazil, the talented author of 'La Defense contre L'Ophidisme,' while admitting that the resemblance between *L. lanceolatus* and *L. atrox* is very close, says "the system of coloration and the characteristics of the venom . . . . constitute the best means of distinguishing them. As regards coloration, I have seen many *Lachesis atrox*, and my experience is that individuals differ in shade, some being light and others darker, but as a rule they are lighter than the only living adult *L. lanceolatus* (St. Lucia Fer de Lance) I have seen. I have, however, seen a large number of very young living Fer de Lance, and so far as my recollection goes, had they been mixed with a lot of young *L. atrox* of the same size, it would have been very difficult to say which was which. I have had specimens of *L. atrox* in my possession for years, and they have gradually become darker with time. It is because of this very little difference—if any exists—between the two species, which Dr. Boulenger thinks may have to be united, that I always call the *L. atrox* of Trinidad 'Fer de Lance,' discarding the Mapepire, which thus becomes exclusively applied to *Lachesis mutus*." If this plan is adopted generally, it helps us to avoid some uncertainty, and if, as Dr. Vital Brazil contends, the poisons of the genera of *Lachesis* differ according to the species, and that each

requires its own antidote, it may well happen that it will become of the utmost importance to the medical man and woodsman to know what kind of a snake bit the patient before applying the specific remedy which is calculated to do the most good. If it can be definitely stated that the creature which caused the trouble was a Mapecire (*L. mutus*) or Fer de Lance (*L. atrox*), a cause of confusion will be removed. For these reasons *Lachesis atrox* is called Fer de Lance throughout this reference.

The Fer de Lance is principally found on the banks of streams, and seems to prefer muddy ones. There used to be places on the Caparo River where they were very common, and were frequently met. When the river was in flood they moved farther away from it, and when it resumed its normal proportions the Fer de Lance returned to its banks. The snake is often to be found in such situations in small bushes five feet or so from the ground. Unlike the Mapecire, the Fer de Lance is most ready to bite when molested, and it will generally put up a fight for life and liberty. Perhaps it is for this reason that most of them do well in captivity, feeding, sloughing, and breeding without difficulty. In a measure they even become tame—that is to say, they soon know the person who feeds them, and anticipate his approach with raised head and expectant air. The young ones quickly learn that a mouse or other dainty usually appears through the sliding trap at the top of the cage, and if it is opened incautiously, they will come half-way through with open mouths and extended fangs. Other and harmless snakes do this also, and from them I have suffered many a bite. Therefore I am careful with the Fer de Lance, which, while not intending to hurt me, in its eagerness to get the tit-bit might inflict a serious injury. But though so ready to bite, if one goes about it in the right way and avoids frightening the snake, or rousing its antagonism, it is easily captured. On one occasion a Fer de Lance was found coiled up at Caparo. Mr. Albert Carr went home, a mile or so distant, and got a kerosene oil box and cover. He nailed the lid to a stick six or seven feet long, and taking another stick of equal length, returned to the sleeping reptile. The box, opening upward, was placed as near the snake as possible, practically within a foot or two. The end of the long stick was inserted gently between the coils, and then the reptile was quietly lifted and dropped gently into the box. To put the cover on afterwards was easy, and five or six Paris points and a hammer secured the deadly reptile, which was thus taken unhurt and without danger. Mapecires have been secured in similar fashion. Another plan is to use a bag with its mouth open like that of a butterfly net. This is placed open behind the snake and close to it, so that if it backs it does so into the bag. With a long stick the snake is gently touched. It at once assumes an attitude of defiance, keeping its eyes fixed on the man with the stick. It gradually moves backward with that circling movement peculiar to the vipers when on the

defensive, and thus goes right into the open bag. When far enough in, it is easy to close the bag with a stick, after which the mouth can be tied up, and the snake is a prisoner. All that is wanted to do this successfully is perfect coolness and a little patience. Rough usage, sudden movements, and teasing will work the *Fer de Lance* into a perfect fury. He will strike at his aggressors again and again, and each time he does so he will spread wide his gaping jaws and extend his formidable teeth. If he is in good condition and has not used his venom for some time, and the poison-fangs are full, he will even send tiny jets of poison from his perforated teeth to a considerable distance. On one occasion, says Mr. Carr, the venom thus ejected struck the face of a woman who was watching the proceedings from a distance of twelve feet. I myself have seen one throw two fine jets a distance of at least six feet. I do not think that the snake intends to perform this feat, for the vipers at least know the value of their venom, and, as a rule, do not waste it. No possible end can be gained by spurting the death-dealing secretion at random. It is only potent when it is introduced into the vascular system, which only occurs because the action of extending the fangs into the stabbing position presses on the over-charged poison-sacs. At ordinary times the resistance offered by the skin of the victim affords the pressure necessary to cause the ejection of the lethal fluid. Many snakes are credited with spitting, notably cobras, ringhals, and mambas, but these ophidians, if I may judge by an Egyptian Cobra I once possessed, are of very different temperament and much more excitable than either of the vipers, *Lachesis* or *Crotalus*. Cobras, ringhals, and mambas are silly goose-like animals, striking aimlessly without provocation, a practice to which the Viperidae are, so far as I know them, not at all given. Roosevelt, in 'African Game Trails,' records an instance of venom-spitting snakes:—

"At this camp we killed five poisonous snakes—a light-coloured tree-snake, two puff adders, and two seven-foot cobras. One of the latter three times 'spat' or ejected its venom poison at us, the poison coming out from its fangs like white films or threads to a distance of several feet. A few years ago the singular power of this snake, and perhaps certain other African species, thus to eject the poison at the face of an assailant was denied by scientists, but it is now well known. Selous had already told me of an instance which came under his own observation, and Tarleton had once been struck in the eyes and for a moment nearly blinded by the poison. He found that to wash the eyes with milk was of much relief." Ch. viii., p. 193.

My cobra only needed me to look at him, and he was in a fighting attitude, and if I only winked my eye he struck at me when I was quite out of his reach. The poison would trickle down the glass front of his box. *Fer de Lance* are not so wasteful, except when their poison-glands are overcharged. It is not often that they strike when the object is out of range. Cobras

have fixed fangs, and in the anatomy of the head are altogether different from the Viperidæ, particularly *Lachesis* and *Crotalus*, and, although exceedingly deadly, are not nearly so sagacious in the use of their terrible powers as are the pit-vipers. A very large Fer de Lance is six feet long. As a rule the adults run from four and a half to five feet. Mr. Ulrich saw one at Woodlands, Gunico, which measured five feet one inch without the head. Its last feed had been a Manicou Gros Yeux (*Didelphys philander*). Fer de Lance feed largely on wood-rats and mice. One that I had for many months and which would not feed got very thin and weak. At last I tried him with frogs, and he took to them kindly, catching them as they hopped past him, though once he went after one and caught it swimming in the water. This snake soon recovered health and strength, and ultimately became a fine animal, feeding on whatever was offered to him. In nearly every country where snakes are found there is a legend that they fascinate their prey, and that they take them when they are in a dazed or hypnotic condition, which is caused by the peculiar powers of the snakes. De Verteuil tells one such story. The victim was a squirrel which was at first observed clinging to the branch of a tree while it screamed and struggled. Then it fell to the ground. The observer of this bit of wild-life tragedy went to the spot and found the poor creature in the jaws of a venomous snake. But this was the end of the story. The beginning is not recorded. The squirrel was probably first struck at and bitten when on the ground. It escaped to the tree, but before it had got far, the poison had taken effect and paralysis had begun, hence the screams. When the victim fell, the waiting snake seized it. Common rats and mice do not seem to be afraid of either poisonous or harmless snakes. Manicou Gros Yeux, and most birds, are certainly afraid, but they are by no means fascinated and deprived of their power to escape—that is, not until they are bitten by the venomous species. The only case of snake fascination of which I know is that of the European frog pursued by the non-venomous ringed snake. The frog seems to be in a terrible nightmare, and loses the power of making his customary wonderful succession of leaps which would soon carry him out of danger. Instead, he crawls as if he had a tremendous weight to drag along. Animals introduced into the Fer de Lance's cage simply concern themselves with trying to get out. Except in the case of the Manicou, there is no hesitation about running over the snake, which, if not in a feeding mood, rats and mice will attack.

The venom of the Fer de Lance is most potent. It acts quickly. Rats are sometimes struck, and drop at once, and with either cramped or stretched-out limbs die in a second or two. At other times the interval before death is slightly longer. The bitten rodent runs about actively, then suddenly seeks a corner, rests quietly for a moment or so, then vigorously washes itself. Next, paralysis sets in, and ultimately it falls over. As a rule the Fer de Lance waits to the last moment and until

death has occurred. He then moves towards the stricken animal, which he has been watching closely. He examines the body all over with flickering tongue; then seeks the head, and as soon as he finds it, begins swallowing at the snout. The venom of the *Fer de Lance* is fatal to other snakes. For many years I had a large South American Rattlesnake which had been brought up from the time it was less than a foot long. He was a big, powerful animal and, like most rattlesnakes, of the sweetest and gentlest disposition it is possible to imagine. One day Mr. Wilfred Walker, the well-known traveller and author, arrived from the country with a large *Fer de Lance*. He wanted to house it until he could get a suitable travelling-box for it, as he was sailing for England the next day. I had no spare box available, and I offered to put the *Fer de Lance* in the rattlesnake's cage, and Mr. Walker assented. The rattlesnake had never seen another snake in his cage since he had become adult, and he got greatly excited. He moved towards the newcomer, which was a lady, with his head bobbing up and down in the queer way which so many reptiles exhibit when courtship afoot. I was called away at the moment, and was gone perhaps an hour and a half. When I returned, Rattles was dead. The *Fer de Lance* had bitten him about the middle of the back and close to the spine. The punctures were plain, and the flesh for more than an inch round the wound had turned soft and pappy. On Sept. 20, 1895, I placed a rather small *Fer de Lance* in a cage with another of the same species but a larger animal. The pair quarrelled at once and bit each other several times about the head. Half an hour later the smaller snake had a much swollen head, and a thin reddish-brown fluid was dripping from the back part of his upper jaw. Both snakes were disinclined to move. On Sept. 21 the swelling on the small snake disappeared. The large snake was not swollen. The small one would not feed for some time, but eventually his health and his appetite returned. On Sept. 30 the large snake was uneasy. At 2.45 p.m. she cast a young one—dead. At 4.45 there was another with a deformed head—also dead. At 5.15 a third—dead. On October 1 there were 23 young snakes, and all dead but one, which was very much alive, self-possessed, and coiled up in a corner. All the young had yellow tails. Their length ranged from 16½ cm. to 27½ cm. The majority were 24 to 26 cm. Five were encased in transparent envelopes. All except the live one, which was 25 cm., had umbilical cords attached. On October 3 another one was born—dead with maggots in it. On the 4th the live one swallowed a tailless anole lizard. On the 5th it devoured a small frog. On October 14 another dead one was born in an advanced state of decomposition. The mother died the same night. On October 14 the young one shed its first skin. On October 28 it ate a small anole. In January 1896 this snake was very vigorous, and killed and ate lizards as often as they were offered to it. On January 30 it struck a mouse twice, and it died within

a minute. There the record ends. The snake lived a long time, and grew and flourished exceedingly. From the foregoing it would appear that the effect of the smaller Fer de Lance having bitten the larger one was to kill nearly the whole of her brood, and to work such mischief in her system that parturition could not be completely effected, with the result that she died, being poisoned by the decomposing young twenty-four days after she was bitten. A pair of *Ancistrodon piscivorus* which I once had frequently quarrelled for a particular spot in their tank. They used to bite each other, and their heads swelled as a consequence, but the inflammation passed off in a few hours. My notes show that young Fer de Lance are frequently born between September and January, inclusive. Besides the thirty in the case just mentioned, I have seen families of twenty-nine (three born dead); thirty-two (eleven born one day and twenty-one two days later, all very much alive); fifty-six (nineteen dead and one aborted egg—two were produced eight days after the others and another fourteen days later, all three being dead), after which the mother died. The Messrs. Carr have a record of 56, but in that case the mother lived.

As was mentioned previously, the young snakes have yellow tails, which they seem to keep for, at any rate, two years. This yellow tail looks like a little caterpillar or worm. The old snakes, when excited or angry, vibrate their tails at a great rate, and the tapping against the herbage makes a very fair imitation of the Rattlesnake's dread but providential alarm. But the young ones do not use their tails thus. They twist and wriggle the yellow little thing, and make it look like a worm. The little snake itself is very inconspicuous amongst dry leaves or on the bare ground, but the wriggling tail used in this fashion acts as a bait to small creatures, which are thus brought within reach of the snake's death-dealing fangs. Twenty years after making this observation, while feeding some newly-born Fer de Lance with some tiny frogs (*Prostherapis trinitatis*) common in the St. Ann's river, I saw one of the snakes wriggling its little yellow tail. A little frog saw it too, and crept stealthily forward, then leaped and seized the tail in his mouth, and pulled determinedly at it. I have no doubt that, had not the owner of the tail been engaged at that moment swallowing another frog, he would have turned and caught the little chap who was trying to bolt his tail. The Trinidad woodsmen say that the mother Fer de Lance crawls along in one direction as she deposits her young ones, and that, when the last one is born, she turns round and retraces her journey, swallowing all the young ones she can find *en route*.

On one occasion Mr. Arthur Carr brought me a fine specimen of Fer de Lance which he acquired in a curious fashion. He saw great excitement in a village shop, and going to ascertain the cause, was astonished to see a man playing carelessly with a large Fer de Lance. He warned the professed charmer of the danger

he ran. The man replied that he had a powerful L'Oraison to protect him. Mr. Carr was an unbeliever, and going nearer, discovered the prayer or charm consisted of a black thread, with which the snake's mouth had been neatly sown up. On one occasion, however, a man brought me in his bare hands a small Fer de Lance which had its mouth and fangs in good working order. The Fer de Lance is a great rat destroyer.

## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. *Epicrates cenchris*.  
 „ 2. *Corallus cookii*.

## PLATE II.

- Fig. 1. Trinidad Anaconda. Length 16 ft. 6 in.  
 „ 2. *Boa constrictor*. Length 12 ft.

## PLATE III.

- Fig. 1. Young *Boa constrictor* killing an Ameiva Lizard.  
 „ 2. *Boa diademata*.

## PLATE IV.

- Fig. 1. *Spilotes pullatus* showing inflation of the neck.  
 „ 2. *Herpetodryas carinatus*.

## PLATE V.

- Fig. 1. *Leptophis loerercus*.  
 „ 2. *Leptophis regine*.

## PLATE VI.

- Fig. 1. *Hydrops triangularis*.  
 „ 2. *Petalognathus nebulatus*.

## PLATE VII.

- Fig. 1. *Trypanurgus compressus*.  
 „ 2. *Leptodira annulata*.

## PLATE VIII.

- Fig. 1. *Oxyrhopus clælia*.  
 „ 2. *Oxyrhopus clælia* swallowing a Fer de Lance.

## PLATE IX.

- Fig. 1. *Oxybelis acuminatus*.  
 „ 2. *Elaps coralinus*.

## PLATE X.

- Fig. 1. *Lachesis* and her eggs.  
 „ 2. *Lachesis atrox*.

## 12. On the Presence of Broadbills (Eurylæmidæ) in Africa.

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(Text-figures 1-5.)

In the 'Ibis' for 1914, pp. 495-502, Mr. G. L. Bates, the well-known African collector and ornithologist, published a paper "to indicate a few anatomical and other characters of the African genus *Smithornis*, hitherto placed among the Muscicapidæ, which prove that it cannot belong to that family, or, indeed, to the normal Passeres at all."

On his return from West Africa at the beginning of 1923 he brought with him two specimens of *Smithornis rufolateralis* in the flesh, together with two embryos of *S. sharpei*, and placing them in my hands desired me to determine the affinities of the genus. In the paper cited above, Mr. Bates, beyond calling attention to the normal passerine form of the sternal spine, did not concern himself with the osteology of the species under notice, but he did examine the syrinx, the deep plantar tendons, and other superficial parts of the bird's anatomy, and although he does not express any opinion as to what *Smithornis* actually is, with the exception of the statement quoted above, it is perfectly clear that what he had in his mind was that it belonged to the family Eurylæmidæ or Broadbills.

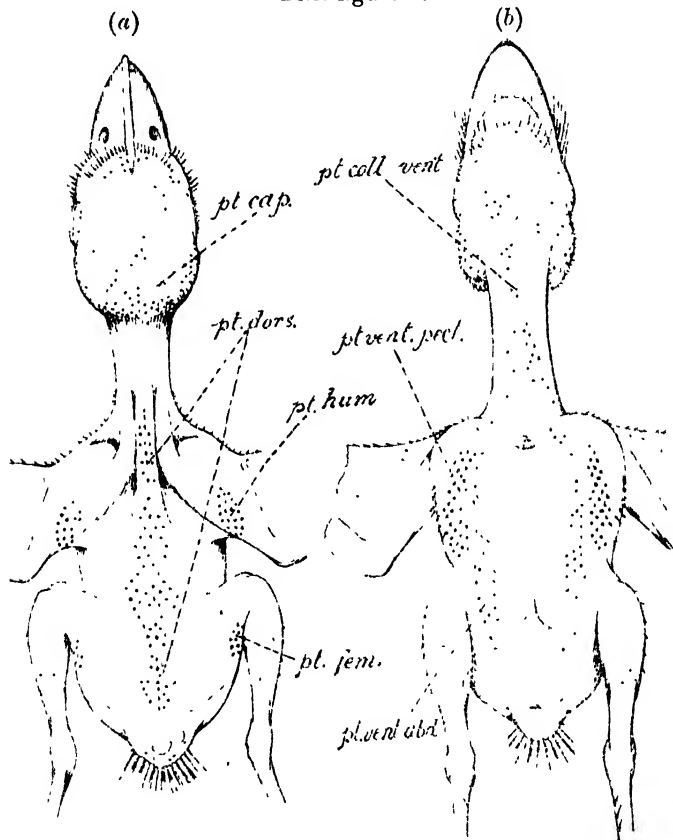
My investigations, therefore, are only confirmatory of what Mr. Bates had previously suspected, but they do, I think, undoubtedly indicate beyond room for doubt, that the African *Smithornis* is none other than a Eurylæmid. As the presence of Broadbills had never, previously to Mr. Bates's paper, been suspected in the African Continent, their former known area of distribution being confined to India, the Malay Archipelago, and the Philippines, the result of my investigations would appear to be sufficiently interesting to warrant these notes. They are, indeed, a remarkable confirmation of the oft-quoted statement "*Ex Africa semper aliquid novi*."

**PTERYLOSIS.**—Not counting the remicle, which is large, there are ten primaries and eight secondaries, and this is confirmed by an examination of the embryo. The wing is eutaxic or quincubital. The rectrices number twelve; the oil-gland is nude, and I can detect no sign whatever of an aftershaft, not even with the aid of a microscope. As already noticed by Bates, the outermost upper major covert is conspicuously longer than the rest.



*Pteryla capitis* (text-fig. 1).—Perhaps the most conspicuous feature here is the very strongly developed row of long rictal bristles extending from the gape almost to the middle line. In addition there are some loreal bristles and a little tuft of white and rather stiff loreal feathers, somewhat similar to, or reminiscent of, those seen in *Sarcophanops* (a *Eurylemid*).

Text-figure 1.

Pterylosis of *Smithornis*: (a) dorsal view; (b) ventral view.

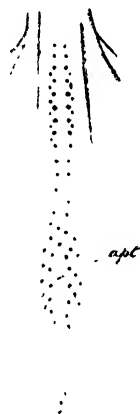
For explanation of lettering, see text.

As will be noted from the figure, the *Pteryla capitis* proper covers in the adult the whole of the upper region of the skull, the tract being evenly distributed (and consisting of somewhat feebly developed feathers) with the exception of two crescentic apteria laterally situated to the inner side of the upper eyelids. In the embryo the arrangement is somewhat different (cf. wood-cut).

*Pt. colli dorsalis*.—This is remarkable from the fact that it does not exist, there being no trace of even degenerate feathers to be observed. This condition also obtains in the embryo (cf. text-fig. 2).

*Pt. spinalis*.—This tract is strong and consists of well-developed feathers. Commencing abruptly at about the level of the acromion it extends as a narrow tract between the scapulæ, and gradually expands to its greatest width some little way anterad of a line drawn through the heads of the femurs. From this point a sharp angle is made, caused by the tract narrowing again in its course to the actual level of the femoral heads, and a little posterad of this, where it expands once more before finally reaching the oil-gland. In the adult there appears to be no hint of an apterion in the mid-dorsal lozenge-shaped area (cf. text-fig. 1), but in an embryo (*Smithornis sharpei*) there is a distinct

Text-figure 2.



Embryo *Smithornis sharpei*. Dorsal feather-tract, enlarged.

indication of one (cf. text-fig. 2). Over the lozenge-shaped area of the feather-tract under notice the feathers are long, well developed, and have conspicuous white bases. These feathers with white bases also extend some little way up into the mid-scapular region. They are present in all the species of *Smithornis* throughout Africa, and are used as recognition-marks (cf. Bates's paper). The white bases are not visible when the bird is at rest, but are capable of being exposed at will by the contraction of the muscle (*Dermo dorsalis* of Shufeldt) which underlies the *Pteryx dorsalis*. I exposed this muscle, and found it to be well developed. It is of remarkable interest that in the Oriental Eurylæmid genera (*Eurylæmus*, *Sarcophanops*, *Cymbirhynchus*, and *Corydon*), there are found in the same situation similar feathers having conspicuous white bases. I say remarkable, because here in

these widely separated Africa and Oriental genera colour-pattern proves itself, as I have elsewhere endeavoured to show in other groups, capable of indicating phylogenetic affinities which are subsequently borne out by deeper-seated structures. From what we now know of the anatomy of *Smithornis*, it is impossible to believe that this little piece of colour-pattern owes its origin in these different Continental genera to the effects of adaptation and selection, acting in a precisely similar way in two such widely separated areas of distribution. On the contrary, it seems evident that colour-pattern in this, as in so many other examples which could be quoted, has a deep-seated origin, pointing to similar chromosomal factors and phylogenetic affinities.

*Pt. humeralis*.—In the specimen from which the accompanying figure was drawn, a female, this tract is feebly developed, the forward portion being unrepresented; judging, however, from another example, it would appear to be doubtful if this variation is constant.

*Pt. femoralis*.—This again is feebly developed, only the anterad portion being present; but neither in this tract nor in the humeral represented in the figure does the deficiency appear to be due to "slipping" and loss of feathers.

As regards the *ventral pteryla* (text-fig. 1) little need be said, beyond calling attention to an unusual tract along the edge of the anterior axillary fold. In the specimen examined it was clearly obvious, although not very strong. I have never noted it before.

**RHAMPHOTHECA.**—The bill and the form and position of the nostrils in *Smithornis* are so similar to those which obtain in *Eurylæmus* that further words seem unnecessary.

**PODOTHECA.**—The acrotarsium is covered with transverse scutes; but the planta differ from normal Passerines as regards their epidermal covering in that instead of scutes we find either smooth roughly hexagonal scales (planta) or more specialised, villous or papillomatous modifications of the scales (under surface of toes). It is to be remarked that this is a *Eurylæmid* disposition and character. The syndactylism characteristic of the toes is identical with that obtaining in the *Eurylæmids*.

**MYOLOGY.**—Under this heading I propose to consider only such points as bear on the affinities of the form under consideration.

(1) *The Deep Plantar Tendons.*—My dissections confirm Mr. Bates's discovery of a vinculum running from the tendon of the *flexor hallucis* to join that of the *flexor communis*. In both specimens which I dissected the vinculum was apparent. It will be remembered that in all the *Passeres*, with the exception of the *Eurylæmidæ*, the *flexor hallucis* is independent of the *flexor communis*. The fact that a vinculum is present in *Smithornis*, as well as in the *Eurylæmidæ*, is a point the importance of which does not need to be pressed. It may be

remembered that Garrod\* in 1877 found a vinculum present in three genera of Eurylæmids, and that subsequently Forbes†, as the result of their joint work on the group, placed the Eurylæmids in a Passerine division—the Dermodactyli—which stands apart from the rest.

(2) *Deltoidæus major*.—I find on dissection that the brevis portion of this muscle in *Smithornis* is confined both in its origin and insertion to the upper part of the humerus. Its lower limit, which is entirely fleshy, does not reach a level as far down as the middle of the bone. It is, in a word, completely fleshy throughout and separated from the longus portion. This latter portion of the muscle has its usual source of origin from the acromion, clavicle, and os scapulare of the humerus, and is inserted by means of a moderately long and somewhat flat or ribbon-shaped tendon at the base of the ectepicondylar process of the humerus. Pycraft‡ has described and figured this interesting muscle in *Eurylæmus ochromelas*, and the similarity between his figure and my dissection in *Smithornis* is very striking. Chalmers Mitchell§, writing of this muscle in the Gruiform birds, says:—"the *D. major* is a progressive muscle in most groups of birds, its insertion gradually creeping down the humerus, a relatively long extension being apocentric, a relatively short archicentric." Since tendons are generally held to be metamorphosed portions of muscle, I should be inclined to agree with Pycraft (*l.c.* p. 75) when he says, in criticism of this statement, "it would seem, rather, as if the archicentric condition were represented by the maximum downward extension and that apocentricity is represented by the gradual reduction of muscular tissue." In both *Smithornis* and *Eurylæmus* the condition obtaining in the muscle can, at any rate, be said to be specialised, so specialised, indeed, that the brevis portion has become potentially a distinct muscle.

(3) *Tensor patagii brevis*.—In the Proceedings of the Zoological Society for 1876, p. 508 *et seq.*, Garrod described and figured the passerine and non-passerine methods of attachment of this patagial muscle. From my dissection of *Smithornis* it would appear that the attachment of this tendon is not quite typical of either. At first sight it would seem as if the mode of attachment was typical of Garrod's Picariæ, in which group he included the Pici Rhamphastidæ and Capitonidæ (*cf.* Pl. xlviii. fig. 1, P. Z. S. 1876), that is to say, after engaging at right angles with the belly of the *Extensor metacarpi radialis longior*, the patagial tendon runs along the fibrous attachment of the extensor, and in doing so is so closely and accurately superimposed upon it that the impression gained is that the patagial tendon has merged entirely with the fibrous attachment of the extensor. In point of fact, this is not so, for with careful manipulation it can be demonstrated that the patagial tendon has a separate existence. Nevertheless,

\* P. Z. S. 1877, p. 447.

† P. Z. S. 1905, pp. 53-55.

‡ P. Z. S. 1880, p. 390.

§ P. Z. S. 1901, vol. ii. p. 629.

it is attached to the same point as that from which the extensor fibres arise, so that it cannot be said that the picture is a wholly normal passerine one\*; while it might be maintained that the arrangement indicates a transition between some Picarian method and the normal passerine one.

SYRINX.—As regards the structure and configuration of the syrinx in *Smithornis*, the similarity to that of *Eurylaimus* is so close (cf. figure P. Z. S. 1880, p. 384, after Forbes), that a detailed description appears to be unnecessary. I can find, however, no trace of any intrinsic muscles. Johannes Muller, as far back as 1846, in a memoir on the vocal organs of Passeres remarked that in *Corydon sumatranus* there were “no muscular fibres on the larynx.” Forbes (l. c. p. 386) says that in *Cymbirhynchus* the single intrinsic muscle is very slender. Bates found them very feebly developed in *Smithornis sharpei*, “so thin as to be made out with difficulty,” and, again, he writes, “of most of the specimens examined I was content to say that no muscles could be made out attached to the lower end of the trachea or the bronchi.” It is interesting to note also that he says: “It was the peculiar noise made by the birds belonging to the genus *Smithornis*, and their apparent inability to utter any kind of song such as most or all Flycatchers sometimes utter, even though usually silent, that led me first to look at the lower end of the trachea and the organ of voice. It was seen at once that the syrinx was bare or nearly bare of muscles lower down than the point where the sterno-tracheal muscles leave the trachea.”

#### OSTEOLOGY.

Under this heading it is not my intention to enter into a long and minutely detailed description of the skeleton of *Smithornis*, but rather to make my account as comparative as possible and, as far as possible, to seize upon only the most important and striking characters. Such a procedure will, it is hoped, enable the reader to grasp far more readily the remarkable resemblances, one could practically say identity, which the osteological characters of *Smithornis* bear to those of the Eurylaimids. Pycraft†, in as far as the material at his disposition allowed, has already fully dealt with these, and this piece of good work renders my task all the more simple and expeditious.

#### *The Skull.*

Although there is a considerable amount of specialisation in the various Eurylaimid genera (judging from the scanty amount of material available in the National Collection), the general conformation of a Eurylaimid skull is striking enough to make its

\* For a normal passerine arrangement, cf. also Shufeldt, ‘Myology of the Raven,’ p. 114, fig. 35.

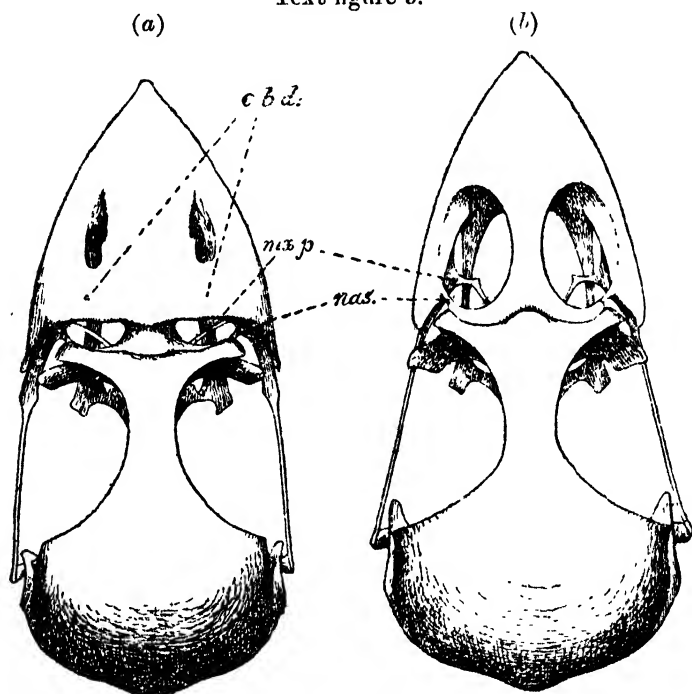
† P. Z. S. 1905, pp. 30–56.

recognition somewhat difficult to miss. In a preliminary superficial survey, perhaps one of the most striking features to be noted is the remarkable nasal hinge and the peculiar disposition of the nasal bones. *Smithornis* exhibits these points to perfection. In the disposition of the nasal bones it is, perhaps, more like *Calyptomena* than any of the other skulls available, but the reduction of the nasals is, in fact, so typical of the Eurylamids as to be obviously comparable with any form I have seen, especially *Cymbirhynchus*; indeed, it is with this genus that the skull of *Smithornis* must be compared in general and in particular; for its resemblances in both respects are little short of amazing. At first sight an inspection of that dorsal portion of the skull in *Cymbirhynchus* anterad of the nasal hinge, is apt to distract our attention from the morphological similarity between the two forms; but this is simply an effect of the specialised ossification which has occurred round the nasal orifices, as well as down nearly the entire length of the nasal and dentary processes of the premaxillae. Had this cavernous bony development taken place to the same extent in *Smithornis* it would have been, so far at least as the skull is concerned, not an easy task to have found characters to have separated the two forms generically. And here we may pause to make what seems to be rather an important point in regard to the general conformation of the bony structure of the premaxilla in the Eurylamids. Pycraft (*l. c.* p. 35) writes as if a hooked tip to this was uniformly characteristic of this group. It may be true of *Calyptomena* and *Corydon*, in which there is a strongly marked hook and a pronounced decurvature of the bill; but in both *Cymbirhynchus* and *Smithornis* the premaxilla is very conspicuously flatter both from side to side and from end to end, while a hook may be said not to exist. The difference is so striking that it seems to suggest that it may be correlated with other differences pointing to the presence of two groups within the family. Coming to that portion of the dorsal aspect of the skull posterad of the nasal hinge, it may be safe to state that *Smithornis* is not only typically Eurylamine but its resemblance to *Cymbirhynchus* is remarkable, especially as regards the proportions of the cerebral dome and its relations to the cerebellum. The interorbital region is not, however, so grooved, and the condition noted is more like *Corydon*. In this region in all the Eurylamid skulls I have examined there is a somewhat remarkable foveated appearance of the bone, and this rather singular condition is faithfully reflected in *Smithornis*. Trifling as this character might seem to be, it is, as a genetic factor, most convincing.

As regards the base of the skull, a comparative study of such important structures as the palatines, vomer, pterygoids, the basitemporal plate, occipitals, exoccipitals, tympanic cavity, maxillary bar, the nasal cartilages, the dentary, palatine, and nasal portions of the combined premaxillaries reveals the surprising fact that there is a closer likeness between *Smithornis* and

*Cymbirhynchus* than between *Calypotomena* and *Corydon*. The likeness between the two former genera is indeed so close as to be very remarkable indeed, especially when we consider that they are denizens of such widely separated regions. A reference to the accompanying figures ought, I think, to be enough to convince the most sceptical that such a similarity between so many important structures cannot for one moment be considered as due to convergence. It is to be noted, however, that the maxillo-palatines differ. In *Smithornis* they commence by passing directly

Text-figure 3.

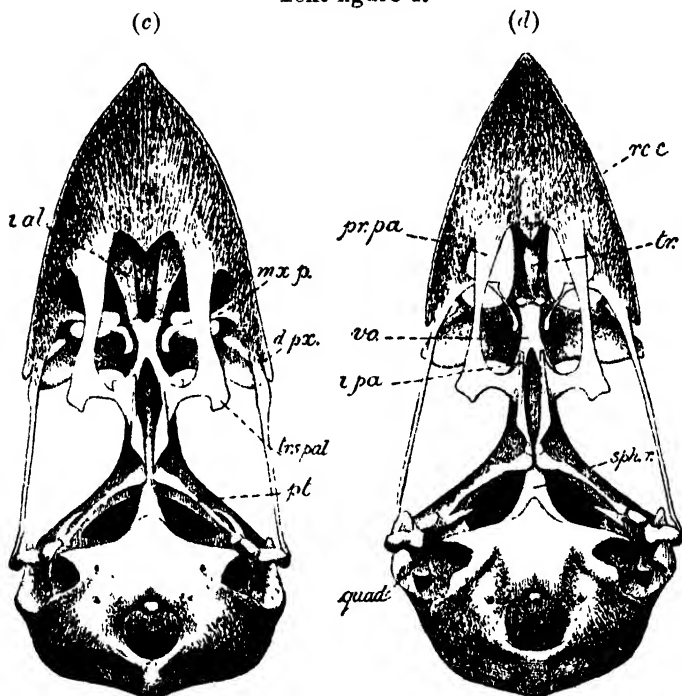


Dorsal view of skulls of:—(a) *Cymbirhynchus*. (b) *Smithornis*.  
*c.b.d.*, cavernous bony development. *mx.p.*, maxillo-palatine processes.  
*nas.*, nasals.

inwards, then, after describing an abrupt angle, they pass inwards and backwards as extremely fine spicules, expanding somewhat towards their termination, as in *Corydon*, and finally being attached by the usual ligamentous bond to the interpalatines. Thus, although typically Eurylæmid, they are not like the condition to be noted in *Cymbirhynchus* (cf. text-fig. 4). In the union of the posterior style-like processes of the vomer with the ethmo-palatines, there is also, in *Smithornis*, a slight morphological

diversity as compared with what is seen in *Cymbirhynchus*, where we have a somewhat conspicuous osseous wing; but this is an unimportant detail. Judging from a specimen in the British Museum, I am of the opinion that in *Cymbirhynchus* the palate is completely ægithognathous. Unfortunately, in the specimen of *Smithornis* the ali-nasal and, indeed, all the nasal cartilages had disappeared, so that it was impossible to form any idea as to the method of attachment of the vomerine cornua with the nasals. It is to be noted, however, that transpalatine processes

Text-figure 4.



Ventral view of skulls of:—(c) *Cymbirhynchus*. (d) *Smithornis*.

*i.al.*, intermaxillary. *mx.p.*, maxillo-palatine process. *d.px.*, dentary process of premaxilla. *tr.spal.*, transpalatine. *pl.*, pterygoid. *rc.c.*, recurrent. *tr.*, trabeculum. *pr.pa.*, prepalatine bar. *va.*, vomer. *i.pa.*, interpalatine spurs or processes. *sph.r.*, sphenoidal rostrum. *quad.*, quadrate.

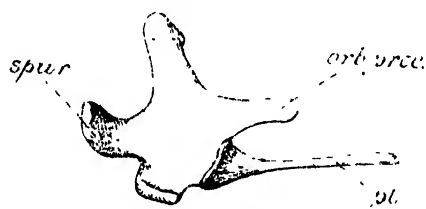
are present on the palatine plates, and this is said to be a sure correlate with complete ægithognathism. What I take to be septo-maxillaries may be noted (*cf.* text-fig. 4) still attached to the vomerine cornua in *Smithornis*, and these doubtless joined up with the ali-nasal cartilages, as is to be noted in the vomer of *Cymbirhynchus* (*cf.* text-fig. 4).



As regards other points in the *Smithornis* skull which should be noted:—The lachrymals, as in *Cymbirhynchus* and all other Eurylæmid genera except *Calyptomena*, are absent: the ant-orbital plates are obviously Eurylæmid, and, indeed, when one takes a glance at this forward part of the orbit and observes these plates, the mesethmoid, the transpalatines, and the post-palatines with their pterygoid attachments, the resemblance between *Smithornis* and *Cymbirhynchus* is very striking indeed: so is the almost complete absence of the post-orbital process and the strong development of the squamosal process and the extent of the temporal fossa.

As regards the *quadrate*, Pycraft (*l. c.* p. 39) has called attention to the fact that in the Eurylæmids, in common with the Tyrannida and some other Passerine forms, this bone sends out a strong spur for the articulation of the quadrato-jugal bar. He says this spur projects like a buttress laterad of the outer condyle for the lower jaw. These conditions are fulfilled in *Smithornis*,

Text-figure 5.

*Smithornis.*

Quadrate (right) enlarged.

whose whole quadrate is an exact replica of that of *Cymbirhynchus*. Nothing could be more convincing than the morphology of this bone in *Smithornis*, and to it one might feel safe in trusting for a sure Eurylæmid verdict.

Enough, therefore, has been already said in regard to the osteology of this interesting form to prove beyond a doubt that *Smithornis* is a Eurylæmid. Nevertheless, there are one or two points in regard to the rest of the skeletal structure to which attention must be drawn.

A good deal of stress, for instance, has been laid upon the simple condition of the *spina externa of the sternum* (*cf.* Gadow\* and Sclater†) as being characteristic of the Eurylæmids. In *Calyptomena* and *Corydon* it is certainly remarkable for its unforked appearance, but in *Cymbirhynchus* there is a distinct tendency to forking. The tendency is there, in more than a latent condition, and in *Smithornis* it is manifest in its full

\* Broun's Thier-Reich, System. Theil, Bd. vi. Vögel.

† 'Ibis,' 1872, p. 177.

**Passerine perfection.** The hypocleideum, however, is large, as in the Eurylemids generally, and anastomoses with the anterior edge of the carina.

*The Coracoid.*—In regard to this bone I can see nothing that does not fit the Eurylemid picture, while as regards the way in which the scapula, furculum, and acromion unite to form the foramen triosseum, the details to be noted in *Calyptromena* (figured by Pycraft) are faithfully reproduced.

I have carefully gone over the rest of the skeletal structure, and much ink might be spilt in describing it if one desired to dot the i's of what has been indicated above. There is one other point, however, which may be noted. Bates, in describing the hyoid of *Smithornis*, drew attention to the shape of the urohyal. He has found that in all the normal Passerines which it has been his custom to examine, this little bone is very flat with a thin border of cartilage at the edges and tip, but that in *Smithornis* it is rod-shaped. I can confirm this observation. As compared with the urohyal of a missel-thrush I find the difference is very obvious.

I find, too, that as regards the hinder limb the main artery is the sciatic.

Taken in conjunction with the almost absolute similarity which exists, in *Smithornis* and *Cymbirhynchus*, between the way in which the pterygoids fuse with the post-palatine processes and ride upon the basi-sphenoidal rostrum; between the strikingly faithful way in which the form and relative position of the palatines, with their pre-palatal bars, ethmoidal plates, and transpalatines, are reproduced; and the wonderful likeness as between the two vomers, the maxillary bars, the dentary and palatine processes of the premaxillæ, and the form and relative position, as regards, other structures, of the antorbital plates, I am inclined to think that one seldom sees in comparative osteology anything more impressive. I say impressive, because when one pauses to reflect upon the vast interval in space and time which separates, at the present day, any two living examples of these African and Oriental Broadbills, and considers, as one traces them back in imagination through millions of years and through countless generations to their common ancestor and common place of origin, that these amazing morphological similarities have been continuously and continuously reproduced with such a wonderful exactitude, not only is one lost in amazement but I am personally free to confess that the idea that such similarities of structure could have been acquired by any cause that was not, so to speak, germinally conceived and inevitable from the start seems equally amazing. If, for instance, we concentrate our attention upon the prepalatal bars, transpalatine and post-palatine processes of the African *Smithornis* and the Oriental *Cymbirhynchus* (cf. fig. 4), or upon such structures as their quadriates, it seems utterly impossible to believe that selection, function, or any other external

or chance factor outside the chromosomal mechanism, could have played anything but a minor part in the origin and preservation of such similarities. Such factors may make themselves felt in the way of a survival value or in various minor or indirect ways, but the moment we imagine it possible that they go much beyond this it seems inevitable that, instead of being able to resolve the zoological world into at least some semblance of order, we should have been confronted with chaos.

Finally, I would like to draw attention to the remarkable and monotypic genus *Pseudocalyptomena* for having, as I believe, brought forward evidence to prove the presence of Broadbills on the African Continent, the question naturally arises, are there any genera other than *Smithornis* represented.

In the 'Ibis' for 1909, p. 690, Lord Rothschild described and figured, from a unique example collected fifty miles west of Russisi, north of Lake Tanganyika, a very peculiar bird for which he created a new genus, *Pseudocalyptomena*, as being very like a *Calyptomena* in appearance, on account of the shape and form of the bill, short tail, and its green and blue colour, a combination of colours which, as Lord Rothschild remarked, is quite unique among African Passeres.

Is this new Central African form (*P. graueri*) actually a Broadbill and not merely reminiscent of one? When Lord Rothschild described this species, from the unique example collected by Grauer in a bamboo forest at an elevation of 6000 feet, the presence of Broadbills had not even been suspected in Africa, and the last thing he would have thought in those days was that his rare and highly interesting find might very possibly be a Broadbill.

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13. Report on the Deaths which occurred in the Society's Gardens during 1923. By N. S. LUCAS, M.B., F.Z.S., Pathologist to the Society.

[Received January 22, 1924: Read February 5, 1924.]

On January 1st, 1923, there were living in the Gardens 758 mammals, 1865 birds, and 664 reptiles.

During the year 483 mammals, 1168 birds, and 866 reptiles were added.

The total of animals which have been in the Gardens during the year is:—

Year.	Mammals.	Birds.	Reptiles, etc.
1923 .....	1241	3028	1030
1922 .....	1155	2904	1093
1921 .....	972	2542	1143
1920 .....	1036	2471	1104

The total of deaths for 1923 is 1295.

The table below shows separately the deaths of mammals, birds, and reptiles, the percentage of deaths to the animals which have been in the Gardens during the year, and in the case of mammals the percentage of deaths of those which have died after living there for 6 months, when they are considered acclimatized.

Year.	Total Mammalian deaths.	Total Avian deaths.	Total Reptilian deaths.	Percentage of deaths of population.			Total deaths of acclimatized Mammals.	Percentage of deaths of acclimatized of population.
				Mammals.	Birds.	Reptiles.		
1923 .	325	641	320	26.1	21.1	31.0	167	13.4
1922	320	585	237	27.7	20.0	21.6	167	14.4
1921 .	208	519	281	21.4	20.4	24.5	98	10.0
1920 ..	333	490	202	32.1	19.8	20.1	167	16.1

It may not be out of place to recall that 1921 was the year in which the summer and autumn were remarkably fine and hot, and to point out that the mammalian deaths were fewer in number both among the newly imported and the acclimatized. The weather, on the other hand, had no apparent effect on the birds.

Table of Causes of Death.

Cause.	Mammals.	Birds.	Reptiles, etc.	Numbers referring to Notes.
<i>Pulmonary disease.</i>				
Bronchitis . . . . .	11	8	5	1
Congestion of lungs . . . . .	40	74	26	
Pneumonia . . . . .	28	38	10	
Gangrene of lung . . . . .	3	0	1	
Abscess of lung . . . . .	2	0	1	
Edema of lung . . . . .	0	2	3	
Pleurisy . . . . .	2	0	0	
Empyema . . . . .	5	0	0	2
<i>Cardio-vascular disease.</i>				
Chronic heart disease . . . . .	1	0	0	
Pericarditis . . . . .	1	1	0	
<i>Disease of Alimentary Tract.</i>				
Stomatitis . . . . .	0	0	7	
Gastritis . . . . .	1	0	1	
Gastro-enteritis . . . . .	16	2	25	3
Enteritis . . . . .	30	195	28	
Ulcer of rumen . . . . .	3	0	0	
Gastric ulcer . . . . .	0	1	1	
Over-distention of stomach . . . . .	0	1	1	
Constipation . . . . .	2	2	1	
Intus-susception . . . . .	1	0	0	4
Intestinal obstruction . . . . .	1	0	0	
<i>Pancreatic disease.</i>				
Pancreatitis . . . . .	3	0	0	5
<i>Hepatic disease.</i>				
Fatty degeneration of liver . . . . .	0	1	1	
Cirrhosis of liver . . . . .	1	0	0	6
Necrosis of liver . . . . .	0	1	1	
Jaundice . . . . .	1	0	0	
<i>Diseases of Urogenital System.</i>				
Nephritis . . . . .	7	12	0	
Salpingitis . . . . .	0	6	2	
Egg-binding . . . . .	0	6	0	
Obstructed labour . . . . .	1	0	0	7
<i>Diseases of Nervous System.</i>				
Paralysis of unknown origin . . . . .	1	0	0	
Hemiplegia . . . . .	1	0	0	
Middle ear disease . . . . .	0	1	0	8
<i>Acute Infections.</i>				
Tuberculosis . . . . .	27	37	1	9
? Tuberculosis . . . . .	1	0	0	
Mycosis . . . . .	0	21	0	
? Mycosis . . . . .	0	1	0	
Septicæmia . . . . .	16	12	7	
Pyæmia . . . . .	5	1	6	
Helminthiasis . . . . .	11	4	5	
Caries of skull . . . . .	0	1	0	
<i>Malignant disease.</i>				
Sarcoma of liver . . . . .	0	1	0	10

*Table of Causes of Death (cont.).*

Cause.	Mammals.	Birds.	Reptiles, etc.	Numbers referring to Notes.
<i>Miscellaneous Causes.</i>				
Inanition . . . . .	7	14	5	
Rickets ..	9	0	0	
Senility .. . . .	0	6	0	
New importation . . . . .	0	35	0	11
Carbon monoxide poisoning . . . . .	1	0	0	12
Under anæsthetic . . . . .	0	1	0	
Fibroma of maxillary antrum . . . . .	1	0	0	13
Dermatitis . . . . .	0	0	2	
Anæmia . . . . .	2	0	0	
Killed . . . . .	28	83	17	
Body destroyed ...	4	19	0	
Decomposed . . . . .	25	37	92	
Not examined ..	22	3	17	
Not diagnosed . . . . .	10	12	27	

The preceding table of causes of death is not markedly different as regards composition to those of the previous years. The numbers in column 4 refer to the explanatory notes below.

1. The number of deaths among the mammals due to bronchitis, congestion of the lungs, and pneumonia, viz. 89, is smaller this year than any of the previous four years except 1921. The figures are :—

1920	113 or 31	per cent. of total mammalian deaths.
1921 . .	55 „ 26	„ „ „ „
1922 . . .	100 „ 33·8	„ „ „ „
1923 . .	89 „ 27·3	„ „ „ „

In the course of investigation of these figures it was noticed that there was a seasonal incidence of deaths from these causes. The seasons were May and November.

An attempt is now being made to correlate the weather and this phenomenon.

2. One case of this occurred in a sea lion. From the empyema a virulent streptococcus was isolated.
3. The mammalian deaths from gastritis, gastro-enteritis, and enteritis have diminished considerably. The table below shows the diminution very clearly. Of the 16 cases of gastro-enteritis, 8 occurred in a short space of time in an epidemic in the Small Cats' House. The epidemic was unfortunately not tracked to its source.
4. This occurred in a squirrel monkey.
5. Two of these occurred in green cercopithecus and one in a potto.
6. The case of cirrhosis of the liver was that of a vulpine phalanger.
7. This occurred in a Grecian ibex.



*Table showing Percentage of Deaths from Enteritis in Mammals in relation to total Mammals in the Gardens and total Deaths occurring among them.*

Year.	Deaths from Enteritis.	Total Mammals in Gardens.	Total Mammalian Deaths.	Percentage Col. I. of Col. II.	Percentage Col. I. of Col. III.
1920 ...	38	1036	333	3·6	11·4
1921 ...	55	972	208	5·6	26·4
1922 ...	69	1155	320	5·9	21·5
1923 ...	47	1241	325	3·7	14·4

8. The case of middle ear disease occurred in a cream-coloured courser. The bird was killed, as it could not control its movements, going round and round in small circles. The right tympanum was found to be completely destroyed and the whole region was inflamed.

9. There is an increase of tuberculosis both among mammals and birds.

The mammalian list is swelled by the inclusion of nine rhesus macaques who came with the disease and in whom it was suspected on arrival. They were isolated, and when one had died and the diagnosis confirmed, they were destroyed. There was also a case in a kangaroo rat. It is doubtful whether tuberculosis in a marsupial has been recorded previously.

Of the 37 cases of avian tubercle, 30 cases came from the Western Aviary, mostly among the doves, pigeons, partridge, and quail.

The reptilian case was that of a teguixin.

10. In a guinea fowl.

11. A hundred Gouldian finches were deposited by a dealer, to see whether direct establishment in an aviary were an improvement on life in cages.

12. A flue got blocked in the apes' houses, and one gibbon—a weakly specimen—was gassed by the fumes. Four chimpanzees and one orang recovered. Two small chimpanzees were unconscious for at least 5 days.

13. This occurred in a goat. It was bilateral, and affected mastication by displacement of the teeth in the upper jaw. The animal was killed.

14. The Larval Development of some British Prawns (*Palæmonidæ*).—I. *Palæmonetes varians*.\* By ROBERT GURNEY, M.A., F.Z.S.

[Received December 29, 1923: Read March 4, 1924.]

(Text-figures 1-11.)

The first mention of the larvæ of *P. varians* was made by Du Cane, who, in 1839, followed the development and gave some remarkably good drawings of the larvæ in different stages. Du Cane observed the transformation of stages 1 to 3, and concluded that there were four stages in all between hatching and assuming the adult shape. He stated also that he was able to observe the hatching of the eggs in pure fresh water and to keep the larvæ alive therein for 5 days.

The only complete account of the transformations of the larvæ of *Palæmonetes* is that of Faxon (1879), who dealt with the American species *P. vulgaris* Say. Faxon distinguished 6 larval stages and at least 7 moults, but the development described by him differs in some important respects from that of *P. varians*.

Boas, in 1880, without giving a complete description of the larval history, figured and described the transformations of some of the appendages.

In 1881 Mayer gave an account of the development of the freshwater form of *P. varians* from which Boas later (1889) was able to make his classic comparison between the development of the two races, which he distinguished under the names of var. *microgenitor* and var. *macrogenitor*.

Sollaud, in a series of papers (1912-1919), has dealt with the effect of the increase of yolk in the egg on development and the effects of temperature, and has distinguished a third physiological variety from Tunisia which he named var. *mesogenitor*. This form, unlike var. *macrogenitor*, has proved to be structurally distinct, and should be regarded as a distinct species (Gurney, 1923).

It will appear from this that, though much has been written about the larval development of *Palæmonetes*, no full account of that of the northern brackish-water form has been published. This may perhaps be considered hardly necessary, but it seems to me that such an account may be of value for more than one reason. In the first place, Faxon's account of the larvæ of

\* M. E. Sollaud's work on the larval development of the Palæmoninæ (Bull. Biol. France et Belgique, lvii. 1923, p. 509) contains an excellent account of the development of *Palæmonetes varians* and also of *Leander serratus*. Unfortunately, my own description was already in print when I received from M. Sollaud a separate copy of his paper.

*P. vulgaris* cannot be taken as applying to those of *P. varians*. Secondly, it is important to know in detail the exact course of development in the Decapoda, and this is extraordinarily difficult to follow. It is notoriously difficult to keep Decapod larvæ alive for more than a few days, and the only way, therefore, of following out the larval history is by taking the larvæ in tow-nets and piecing the series of stages together. In the case of *P. varians*, not only can an abundance of material be obtained with ease and certainty, but it is possible to keep the larvæ alive from hatching to maturity, and it is therefore easy to follow the development from moult to moult. Further, as the series of stages is fully as long as in the majority of Caridea, it provides a remarkably good example of Caridean metamorphosis with which others can be compared.

I believe that a knowledge of the larval history is of importance in tracing the systematic relationships of the Decapoda, and that it is essential for this purpose that we should have the information for at least representative species within each family. As I have been able to study the larvæ not only of *Palæmonetes varians*, but also of three species of the genus *Leander*, I propose to deal with the latter in a subsequent paper, wherein comparison will be made between the larvæ of the Palæmonidæ and those of other Caridea.

*Palæmonetes varians* is commonly found not only in brackish ditches without direct communication with the sea, but also in pools on salt marshes and in creeks subject to tidal influence. It is by no means unusual for the salt marshes to be flooded by high tides in summer, and on such occasions the larvæ must be swept out to sea in large numbers. In June 1922 every such pool at Wells swarmed with larvæ, but on July 25 scarcely one was to be found, a high tide having overflowed the marshes in the interval. The larvæ must therefore be capable not only of withstanding great and sudden changes of salinity, but also of completing their metamorphosis in the sea, and it is to be expected that they may occur occasionally in the plankton from the open sea, though, so far as I am aware, they have not actually been identified in such collections.

The salinity of the pools in which the prawns live is, of course, very variable. In ditches near Breydon Water, larvæ were found in water with 6.83 grms. Cl per litre, while at Salthouse the salinity was 14.56 grms. per litre. The marsh pools at Wells were not analysed, but were found on June 20 to have a density up to 1025, or very nearly that of sea-water.

In normal circumstances the struggle for existence must be intense and the destruction of larvæ enormous, since the pools in which they occur are often barely a yard in diameter and have to support the progeny of several females. In such cases a single sweep of the net brings up a thick mass of larvæ. Yet, by the following summer, such a pool will be tenanted by perhaps

half-a-dozen prawns. Such conditions of existence would, one would think, tend to favour an abbreviation of development, and it may be that it is only the frequency of high tides flooding the marshes that has prevented the acquisition of the type of development characteristic of the land-locked fresh-water form of the species.

### Larval History.

The size of the eggs of *P. varians* occurring in salt or brackish water is known to be very much less than that of the fresh-water form of South Europe and North Africa, as follows:—

Danish coast .....	·7-·8 mm. (Mortensen).
Northern form .....	·75 „ (Boas).
Southern form .....	1·5-1·75 „ (Boas).
	1·3-1·4 „ (Sollaud).
Tunisia .....	1·1-1·2 „ (Sollaud).

In accordance with these differences, which depend upon the amount of yolk contained in the egg, the larva is hatched as a true zœna or in a stage combining the characters of the larva and the adult. (Boas, Sollaud.)

In Norfolk, *P. varians* bears eggs somewhat larger than the sizes given by Boas and Mortensen, varying from ·9 to 1·2 mm. in advanced stages. It might therefore be expected that the larval form would partake of the characters of the southern *Palæmonetes*, and hatch in a stage much more advanced than the zœna. Such is, however, not the case. The larva hatches as a zœna of the usual Palæmonid type, with the exception that the pereopods are more developed than is the case in other species, and it passes through a series of stages at least equal in number to those of *Leander fabricii* for example\*. There are normally six stages, corresponding to five moults, before the adult form or first post-larval stage is assumed, but there may occasionally be seven or even more. In the unfavourable conditions of life in aquaria larval development becomes prolonged by additional moults, and it is impossible to recognize definite stages. I have in no case seen, either in nature or in aquaria, any intermediates between stages 1, 2, and 3, which are always produced at the first and second moult respectively, but from stage 3 onwards the changes between moults become so inconsiderable that there cannot be said to be any true metamorphosis.

Sollaud has (1919) studied the larval history of *P. varians*, and finds that the number of moults and the duration of larval life varies considerably with temperature and salinity, but, so far as my observations go, I am inclined to attach more importance to food in determining the course of development.

\* Coutière (Bull. Inst. Oceanog. civ. p. 62, 1907) has already pointed out that the degree of development reached by a larva on hatching does not necessarily influence the number of stages passed through, and *P. varians macrogenitor* has as many larval stages as *P. v. microgenitor*. The only difference in this and other cases is that the changes from stage to stage are less marked.

The larvæ can be quite easily kept alive in aquaria, and I have even kept single specimens for a considerable time in tubes 7.5 cm. by 2.5 cm. without change of water; but the difficulty of providing suitable food and of renewing the water has in most cases prevented me from keeping the larvæ through the whole series of moults, and I attribute the large proportion of "intermediate" stages to the bad conditions provided. These intermediates will be described below.

### The Larva before hatching—embryonic cuticle.

The embryonic cuticle is entirely thrown off before emergence from the egg, but can be studied in larvæ removed from the egg some days before hatching. The appendages are covered by the cuticle in the form of simple bags without indications of any setæ. The cuticle covering the telson, however, has large, pointed lobes corresponding to the setæ of the larval telson, with the exception that the two innermost setæ are enclosed in the same lobe (text-fig. 10 D). That is to say, the embryonic telson possesses only six of these conical lobes in place of seven, which is the number found in the *Brachyura* and is the normal number of setæ on the larval telson in the *Caridea*. Mayer supposed that seven was the primitive number for all Decapoda, but this is certainly not true for the *Caridea*. I have found the embryonic telson of *Pandalus borealis*, *P. montagu*, *Pandalina brevirostris*, *Hippolyte varians*, *Philocheras fasciatus*, and *Caridina simoni* to have six embryonic spines only, as is the case also with the British species of *Leander*. The telson of the unhatched larva is so folded as to appear deeply cleft.

I have been unable to trace any segmentation in the cuticle corresponding to the segmentation of the abdomen in the larva.

### Description of the Larvæ.

#### STAGE I. (Text-fig. 1 A & B.)

The size of the larvæ when hatched varies rather markedly, both in specimens from the same pool and also in those from different localities or adjacent pools. The following average measurements illustrate this variation:—

Wells.	Pool 1 ...	3.2-3.75 mm.,	average	3.55 mm.
	" 2 ...	3.4-3.65 "	"	3.51 "
Blakeney.	" 1 ...	3.6-4.0 "	"	3.8 "
	" 2 ...	3.85-4.1 "	"	3.9 "
	" 3 ...	3.5-3.75 "	"	3.62 "

These differences in size are not accompanied by any differences in structure.

#### Colour.

The general colour of the larva seen under a low-powered lens is straw-coloured with a tendency to orange. In later stages the

colour changes to a distinct orange. Before hatching, and in some cases afterwards, there is a delicate diffuse blue tinge on the surface of the greater part of the body; but this is seldom traceable for long after hatching. As is the case in so many Decapod larvæ, the colour of the chromatophores is not the same in transmitted as in reflected light, and the general colouration is very greatly affected by the degree of expansion of the chromatophores. Larvæ hatched in my aquaria and kept in a strong diffused light became and remained practically colourless, the chromatophores of the thorax and anterior segments of the abdomen contracting so much that they were often difficult or even impossible to see.

The chromatophores may contain only transparent orange pigment, which expands into an exceedingly delicate network of branches. The scattering of the pigment is often so great that the chromatophore itself disappears, leaving only a faint diffuse colour over the area covered by its ramifications. This is commonly the case in the lateral chromatophores of the carapace and those of the abdomen. But many, as for example the large median spot of the third abdominal somite, contains a central nucleus of opaque yellow pigment which expands into thick branches and is black in transmitted light.

The distribution of the chromatophores is shown in the accompanying figures, and it is not necessary to enumerate them precisely, though the position and numbers of them are a valuable aid to identification. I will only draw attention to three points:—

(1) The characteristic feature of the larva of *P. varians*, by which it may be recognized immediately when alive, is a long streak of orange pigment extending down the middle of the telson and widening out at its posterior margin. This streak sometimes breaks up into separate spots, but I am unable to say whether it represents a single chromatophore or several. Probably it is a single one.

(2) In the mouth region a pair of labial and of maxillary chromatophores are generally visible (text-fig. 1 B), but they are very small, and one or both of each pair may apparently be absent. They are *never* sufficiently large to affect the colouration. This is an important difference between this species and the *Leanders*.

(3) The pleon segments have no chromatophores on their ventral surface, with the exception that there is sometimes a small opaque yellow spot at the base of the telson.

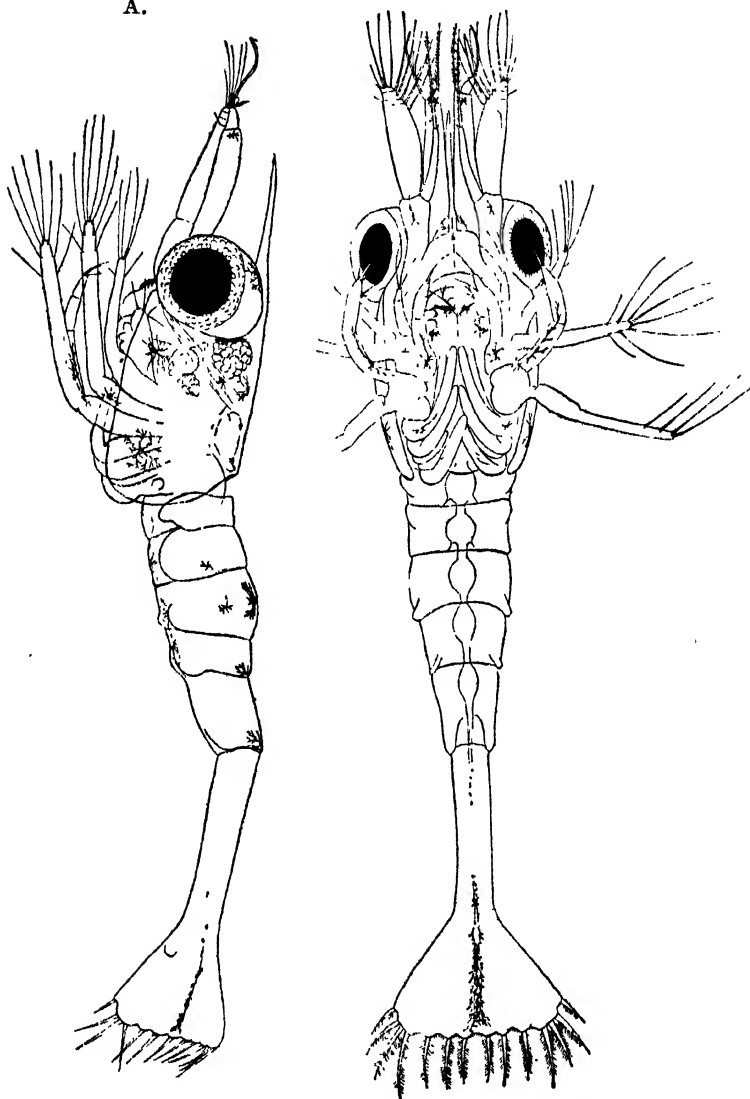
### *Structure.*

The thorax, from tip of rostrum to posterior margin, is scarcely more than half the length of the abdomen, and the carapace lacks any of the spines which are characteristic of later stages. The rostrum is long, slightly downcurved at the end, and the end is sometimes armed below with two or three small

Text-figure 1.

B.

A.

*Palæmonetes varians.*

Stage I.

hooks; but these hooks are minute and often absent. The rostrum reaches nearly to the end of the antennular peduncle.

The eyes, as is always the case in the first stage of Caridean development, are not stalked or movable.

The segments of the abdomen are without any spines. The telson, which is fused with the sixth somite, is broadly equilateral, and bears 14 setæ, of which the 3rd and 4th\* are the longest. The outer two setæ are ciliated on the inner side only, the remainder on both sides.

### *The Appendages.*

The 1st antenna has a long one-jointed peduncle, bearing at its apex a single long feathered seta which is seated on a small papilla. There is no trace of an inner branch, but the outer sensory branch is represented by a small joint bearing three aesthetes, one of which is stouter than the other two. It carries also a short ciliated seta and a delicate seta inserted on the inner side but bending outwards across the aesthetes.

The 2nd antenna consists of a short, strong stem bearing two branches, the scale and flagellum. The former is nearly parallel-sided and jointed at the apex, bearing 10 ciliated setæ. There are, in addition, a minute terminal hair and a delicate outer seta on the first line of segmentation. The flagellum is represented by a narrow rod, about half as long as the scale, bearing a long ciliated seta and a small tooth.

Mandibles. The mandibles are not exactly symmetrical in the arrangement of spines, but on both sides show an indication of a division into molar and cutting parts by an indentation in the middle.

Maxilla 1. Consist of a proximal and distal lobe armed with strong spines and a short endopodite of one joint, bearing a single terminal seta. The distal lobe has no outer seta.

Maxilla 2. The protopodite bears three inner lobes only, two of which belong to the basipodite. The endopodite is not segmented, having a single setiferous inner lobe and one terminal seta. The exopodite or scaphognathite is of the usual Caridean form, with 5 setæ (text-fig. 10 A.)

Thoracic appendages. The three pairs of maxillipedes are fully developed, with large swimming exopodites bearing 6, 8, 8 setæ respectively. The endopodite of the 1st maxillipede is small and one-jointed, with a few slender setæ, while those of the 2nd and 3rd are four-jointed, ending in strong claws.

Behind the maxillipedes are distinct rudiments of the five pairs of pereopods, the first four being biramous. The 1st, 2nd, and 5th are very much larger than the 3rd and 4th, and there is a rudiment of a single gill above the 5th leg.

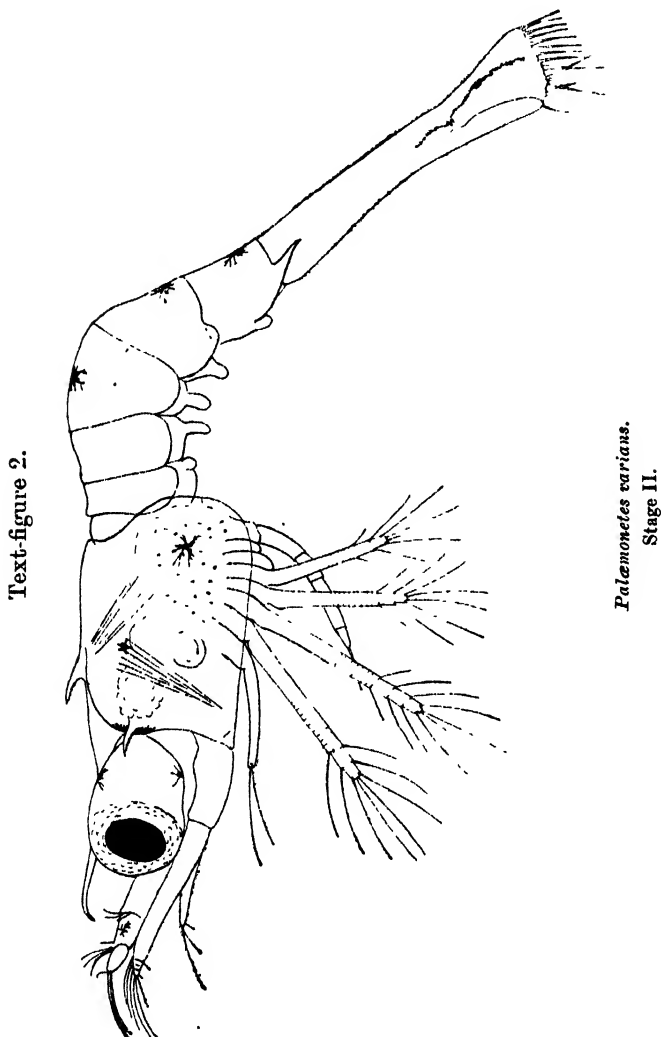
Pleopods. Although the pleopods are not yet developed, they are traceable as minute papillæ on segments 2-4.

\* The setæ of the telson are, in all cases, counted from the outer margin.



## STAGE II. (Text-fig. 2.)

The first moult to stage 2 takes place about 4 days after hatching. Specimens reared in aquaria are almost colourless,



except for the characteristic yellow streak in the telson, but those taken in marsh pools are of a rich orange colour. The arrangement of the chromatophores is the same, except that

there may be one or two additional small centres laterally in the thorax.

Length: Wells, average 3.83 mm.  
Blakeney, „ 4.25 mm.,

i. e., an increase of about .5 mm. in each case.

With the first moult the larva changes considerably in appearance. The eyes are now stalked and movable; the rostrum, which reaches about to the end of the first joint of the peduncle of the 1st antenna, is slender and either straight or more or less bent downwards into a hook at the end. This hook is less pronounced than in *Leander longirostris* or *L. squilla*. On each side of the base of the rostrum is a large toothed supra-ocular spine, and there is a single large toothed median dorsal spine about the middle of the carapace. The 5th abdominal somite has now two long lateral downcurved spines which are retained through later stages. The 6th somite is still not separated from the telson.

The telson differs from that of the first stage very slightly in shape, but the 2nd seta is now ciliated on both sides and there is a pair of additional small median spines—16 in all.

The pleopods are distinctly visible as small buds, those of segments 2-4 being the largest, but there seems to be considerable variation with regard to the size of these buds, which in some cases are merely minute papillæ and in others comparatively large buds.

The peduncle of the 1st antenna is now distinctly two-jointed, and a circle of sensory setæ marks the position of the future third joint. The first joint is slightly dilated at the base. The outer ramus is still one-jointed, bearing 4 aesthetes.

The endopodite of the 2nd antenna is unchanged in shape, but has lost the long terminal spine and small tooth and has two delicate terminal setæ instead. The scale has 17 setæ.

The pereopods are greatly developed as compared with stage 1. The first and second are biramous appendages with functional exopodites resembling maxillipedes 2 and 3. Legs 3 and 4 are still rudimentary, but distinctly biramous and turned forwards along the ventral surface. Leg 5 is uniramous, large and well-developed, being turned forwards and reaching with its terminal spine nearly to the mouth.

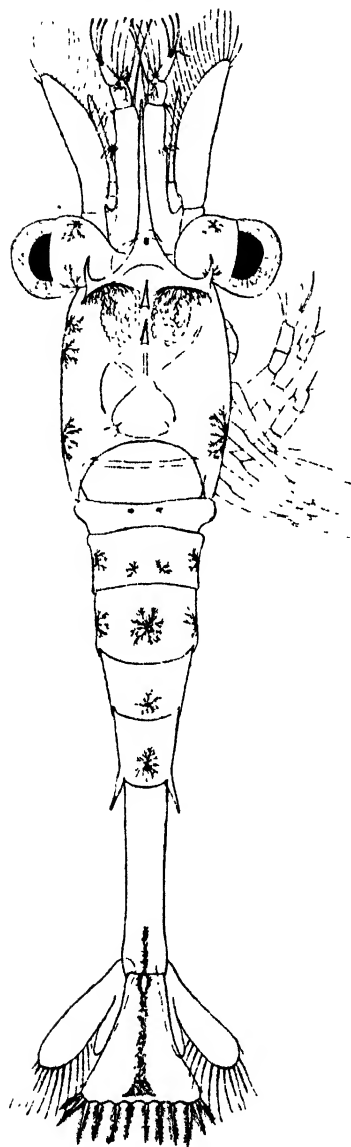
Rudiments of gills are visible upon the pleura of each of the five pairs of pereopods, that of the 5th being considerably the largest.

### STAGE III. (Text-figs. 3, 4 A & 4 B.)

Length: Wells, 4.38-4.9 mm.  
Blakeney, 4.77-4.92 mm.  
Reared in laboratory, 3.65-3.9 mm.

The second moult takes place 4 or 5 days after the first, and  
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Text-figure 3.



*Palæmonetes varians.*  
Stage III.

introduces considerable changes in the larva, which is readily recognized by the possession of two dorsal median spines.

The colour does not differ from that of previous stages and the arrangement of the chromatophores is the same.

Text-figure 4 A.



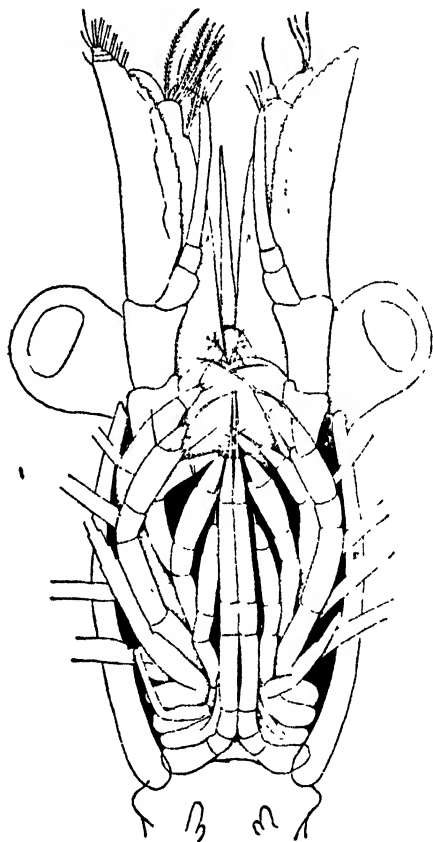
*Palaeomonetes varians*.  
Stage III. Side view.

The telson is now separated from the 6th abdominal somite and is more elongated, the greatest width being about equal to its length. The posterior margin bears the same number of

spines as in stage 2, but the outermost is reduced to a small tooth situated a little way up the outer margin.

1st antenna. The peduncle is still two-jointed, but it is broad at the base with a pronounced external notch. The inner branch is now represented by a distinct joint bearing a single seta. The external branch is unchanged.

Text-figure 4 B.



*Palæmonetes varians.*

Stage III. Ventral view of thorax showing arrangement of appendages.

2nd antenna. The scale still shows traces of jointing at the end and has a larger number of setæ. The inner branch or flagellum is about two-thirds of the length of the scale and consists of three joints, two short basal joints and one long distal joint bearing a few short setæ at the end. The peduncle

is one-jointed and the tubercle on which the antennal gland opens is present.

**Pereiopods.** All the thoracic legs are now present. In the first and second pairs the propodite is slightly produced to form the incipient chela. The third leg is well-developed with a setiferous exopodite, but is much smaller than the second. The fourth remains a biramous rudiment. The fifth leg has developed into the form of a very long styliform appendage bent forwards along the middle line and reaching with the terminal spine as far as the base of the antenna. The great development of this appendage recalls the larva of the Alpheidæ.

**Pleopoda.** These are now present on all somites. On the 1st and 5th they are still small rounded knobs, but on somites 2, 3, and 4 they are forwardly-curved unjointed rods.

**Uropods.** The uropods appear at this stage, the exopodite being large and provided with a number of setæ, while the endopodite is without setæ and about half the length of the exopodite.

**Gills.** All the pleurobranchs are present, but not functional.

#### STAGE IV. (Text-fig. 5.)

Length 4.5-5.4 mm.

After the third moult the separation of definite stages in development becomes exceedingly difficult, since there is so much individual variation in the amount of change taking place between successive moults. This is especially the case with larvæ kept in aquaria, and is, in their case, no doubt due to unfavourable conditions; but even in natural conditions every possible intermediate stage may be found leading in unbroken sequence to the adult form. It is possible to define as the typical mode of development three stages intervening between stages 3 and the post-larval stage, corresponding to three moults, but the number of moults and of intermediate stages may add three or more to these. These three stages I define as stages 4, 5 A, and 5 B.

Stage 4 in its typical form differs from stage 3 as follows:—

(1) An additional dorsal spine appears at the base of the rostrum, making three dorsal spines. The first of these three is retained in the adult, while the other two are lost later.

(2) Pereiopods 1 and 2 are chelate, the propodite having extended nearly or quite to the end of the dactylus. The first pair is larger than the second.

(3) The fourth pereiopod is developed, but the exopodite is often without setæ. Legs 3 and 4 are smaller than 2 and 5.

(4) The pleopods are longer and curved forwards. The 5th are small, but the others are rather large and have rudiments of the endopodites.

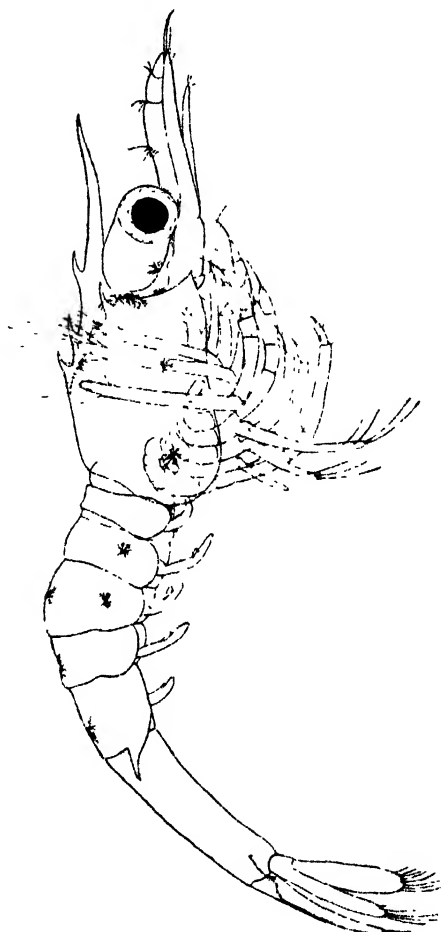
(5) The telson is narrower at the end, the length considerably exceeding the greatest width (sometimes 2 to 1).

(6) The two outermost setæ of the telson are reduced to

minute denticles which have moved a little up the sides, but both form and arrangement of spines at this stage are very variable. There are usually five pairs of terminal setæ (7 pairs in all).

(7) The endopodite of the uropods bears setæ.

Text-figure 5.



*Paleomonetes varians.*  
Stage IV.

(8) 1st antenna. The base is more distinctly notched, and there are usually two "otic" setæ seated in the notch.

(9) The 2nd antenna differs little from stage 3. The endopodite still consists of three joints and is shorter than the scale. The latter has lost all traces of distal jointing. The peduncle

shows an oblique line of division below the insertion of the endopodite. This is the first indication of the separation of a portion of the coxopodite to give rise to the sclerite, which, in the adult, forms apparently the first joint of the flagellum, but is really a part of the peduncle.

Between stages 3 and 4 intermediates are found having every possible combination of characters. In particular, the endopodite of the uropods may be either without setæ, but nearly as long as the exopodite, or may have a very few setæ, or, in a typical form, may have a number of setæ along the inner edge. The telson may be expanded as in stage 3 or reduced in width in various degrees. In one specimen from Cley measuring 6 mm. (larger than normal) there were only two dorsal spines, the endopodite of the uropods was without setæ but as long as the exopodite, and the telson was armed as in stage 3, though slightly narrower. Yet legs 3 and 4 were developed as in stage 4, and the pleopods were also large.

#### STAGE V. (Text-fig. 6, A & B.)

Between stage 4 and the post-larval condition the larva appears as a rule to moult twice, so that stage 5 may be divided into two sub-stages, 5 A and 5 B, but this is not invariably the case. I have, in one instance, been able to observe the moulting of an individual from stage 4 to stage 5 B, and from that to post-larval, but in all other larvæ kept under observation an additional moult has given rise to the intermediate form 5 A. One larva kept from stage 1 in a small glass passed through the first four stages at intervals of 3-5 days. It then moulted, first to a stage intermediate between 4 and 5 A, then to stage 5 A. After two further moults it died, being then still in stage 5 A. It is curious that in this case moulting still occurred at intervals of a few days, yet without apparent growth or change. Under natural conditions stage 5 A is found to be nearly as frequent as 5 B, indicating that two moults are the general rule.

Stages 5 A and 5 B differ together from stage 4 in the following characters:—

(1) Antennæ. The endopodite is longer than the scale, and the distal part has three or more joints.

(2) The telson is much narrower, the width less than half the length, and the greatest width is in or in front of the middle. There are five pairs of distal spines and two pairs of small lateral spinules.

(3) Pereiopods 1 and 2 are larger and fully chelate, but there is some variability as regards these appendages which may sometimes be only subchelate.

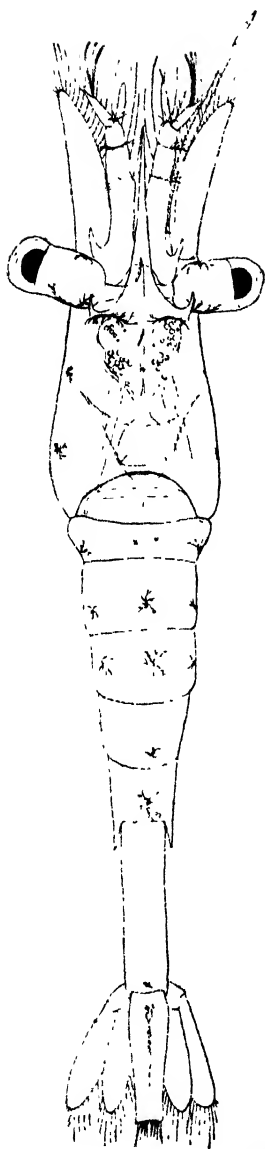
(4) The pleopods are longer.

The differences, in fact, which appear as the result of moults after stage 4 are differences of degree, and not due to the acquisition of any new characters.

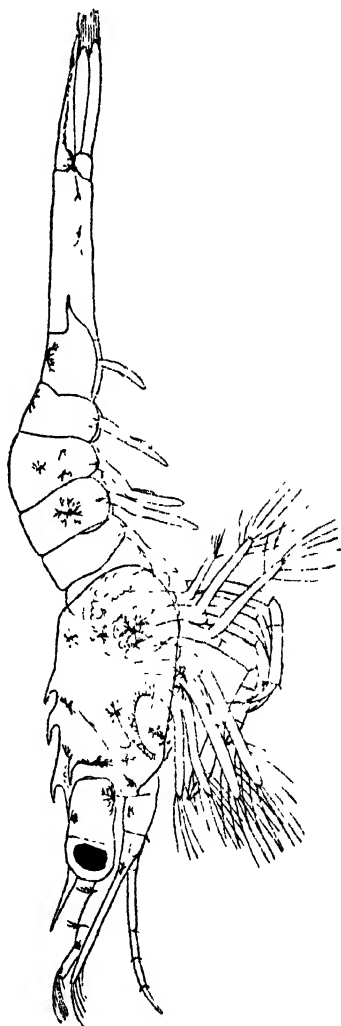


## Text-figure 6.

A.



B.



*Palæmonetes varians.*  
Stage V. B.

Stages 5 A and 5 B are distinguishable only by very small differences:—

(1) Size. 5 A : 5–6·27 mm. 5 B : 6·54–7·2 mm.

(2) The flagellum of the antenna, which in 5 A is but a little longer than the scale and consists of 5 joints, is considerably longer than the scale and of 7–9 joints in 5 B. The long, slender flagellum of the latter stage is an easily recognized and distinctive character.

(3) The telson in stage 5 B is more than three times as long as it is broad, whereas in 5 A it may be a little more than twice as long. The arrangement of spines is the same, with the exception that there is often an additional pair of lateral spinules, which is apparently a new acquisition in 5 B.

(4) The pleopods, which in 5 A are somewhat curved, are long and straight in 5 B.

When the larva in stage 5 A is approaching the moult, it is easy to determine whether it will moult direct to post-larval or will pass through the intermediate stage 5 B. In such cases, if stage 5 B is to arise from the moult, the new telson with its spines will be seen to conform to the old, and the spines on the carapace will also be in process of renewal. If, on the other hand, an individual of stage 5 A or 5 B is found in the moult to the post-larval condition, it will be seen that only the first dorsal spine encloses a new spine, the two posterior spines and the supra-ocular spines being empty. The new telson also does not conform to the old one, having a small median point and one pair of large spines which are being withdrawn from the outermost large spine of the larva. I have not been able to satisfy myself as to whether the median pair of setæ of the post-larval form correspond to one of the pairs of the larval telson. It seems likely that the feathered setæ of the adult telson, which are usually two in number, but may be as many as six (see Gurney, 1923, p. 117), are new acquisitions, and have nothing to do with the larval telson.

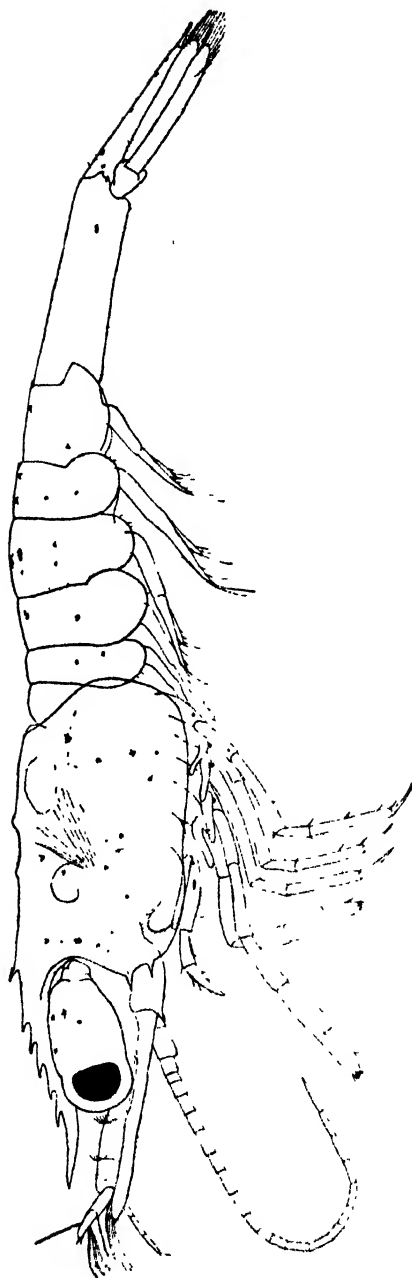
In stage 5 the sclerite between the 1st segment of the abdomen and the thorax ("intermediate plate" of Calman, 1904) becomes chitinized and distinct. At the moult it is cast off attached to the abdomen, of which it is a part, but is easily detached from it.

### First Post-larval Stage. (Text-fig. 7.)

Length 7·07–7·6 mm.

With the moult from stage 5 B the general appearance of the adult is assumed, and the young prawn, though a ready swimmer, changes entirely its means of locomotion. Whereas the larval stages always swim on their backs by means of the exopodites of the legs, the post-larval stages, even if still provided with exopodites, swim mainly by means of the pleopods, and always "right way up." The latter change is no doubt due to the development of the otocyst, since the larva, which is not provided with one, is unable to overcome the action of gravity which naturally causes

Text-figure 7.



*Palæmonetes varians*.  
First post-larval stage.

the body to assume a position with the dorsal side downwards. The presence of sand-grains in the otcocyst does not seem to be necessary for its proper functioning, since I have seen young prawns with the otcocyst entirely empty, but apparently not in any way affected as regards powers of orientation.

I should point out that *P. varians*, more it seems than other prawns, is throughout life an active swimmer. Around the edge of marsh-pools at Wells I have seen clouds of young prawns hovering, as it were, with head upwards awaiting food, and the adults may be seen constantly swimming to and fro in pools by sluice doors and the like. *L. squilla*, on the other hand, is rarely seen to swim unless disturbed.

### Colour.

The young prawn is almost colourless to the naked eye, but with a large number of small chromatophores scattered over the body, of which the distribution is as follows:—

(1) Eye. One yellow chromatophore ventrally, 3 small orange and one large brownish one dorsally.

(2) Rostrum quite colourless.

(3) 1st antenna. One yellow chromatophore in each of the three joints of the peduncle.

(4) 2nd antenna. A few minute pigment spots at base of scale and in stem.

(5) Thorax dotted with small orange chromatophores, not arranged in lines. A large chromatophore runs across the junction between the eyes, which is black in transmitted light, but with an opaque yellow centre in reflected light. No others of this type are found in the thorax at this first stage. No chromatophores were seen ventrally.

(6) Abdomen. Is also dotted over with small orange pigment spots, but there are also in somites 1-3 opaque spots as described under (5). Possibly these are the white spots of the adult. No ventral chromatophores except in somite 6.

(7) Telson with a row of 5 yellow chromatophores down the middle line and one between the uropods and at the end of the 6th somite ventrally.

(8) One chromatophore in the ischiopodite of each of the 5 legs, and also in the 2nd and 3rd maxillipedes.

The changes which take place at the moult to this stage are as follows:—

(1) The rostrum. While retaining the narrow sabre-like rostrum of the larva, the dorsal and ventral teeth of the adult are acquired. The full number of teeth is found in this first stage, and seems to remain as a rule the same throughout life, with the exception that the apex is never bifid at this stage. I have traced the history of the rostrum in a number of specimens, but in most cases for less than four moults. In one case only the apex became bifid at the first moult, while the only

other specimen which acquired this apical tooth under observation did so at the 6th moult. I have met with one case in which a rostrum with, at first, five dorsal teeth, had, after the 5th moult, only four. In all other cases of moults either of young or adults, in this or in other species, I have found the rostral formula to remain the same.

(2) The supra-ocular spines and the two posterior dorsal spines of the larva are lost, while the anterior dorsal spine is retained. The antennal spine which is now present is a new acquisition. The retention of the supra-orbital spine in some Pontoniinæ (e.g. *Periclimenes spiniferus*) is no doubt a primitive character.

(3) The telson (text-fig. 10 E). The shape of the telson remains almost the same, but the posterior margin has a very small median point. The adult form with triangular apex is not acquired until the 3rd or 4th moult. At the outer angles there is a pair of long spines flanked by a pair of very small spines, these two pairs representing the outer two pairs of the larva and the two strong terminal spines of the adult. Whether the median feathered setæ of the adult are new acquisitions or correspond to any of the larval spines I am unable to say. I have examined a number of larvæ about to moult without being able to find any evidence that any of the larval spines other than the two outer pairs are retained. Only in one instance did the third spine appear to contain a delicate new hair. In any case the telson of the first post-larval stage may have no hairs at all, or it may have a pair of very small delicate hairs. In one case I have seen three pairs, in which case it is allowable to suppose that all the larval spines were represented.

(4) 1st antenna (text-fig. 9 A). The antennular peduncle is of the adult form, with the exception that the outer distal expansion of the first joint is only indicated by a small hook-like projection bearing a single hair. The adult form is not complete till about the fifth moult. The inner flagellum consists of 2 or 3 joints only, while the outer shows no trace of the accessory flagellum, consisting of three thick basal joints and one slender distal joint. The growth of the flagellum is dealt with below. The otocyst is fully formed, but is widely open.

(5) The epimera of the 5th abdominal somite are never completely rounded as in the adult, and are occasionally produced into long-pointed processes as in the larva. In some cases these processes are retained through one or more moults, but they are generally lost at the first moult.

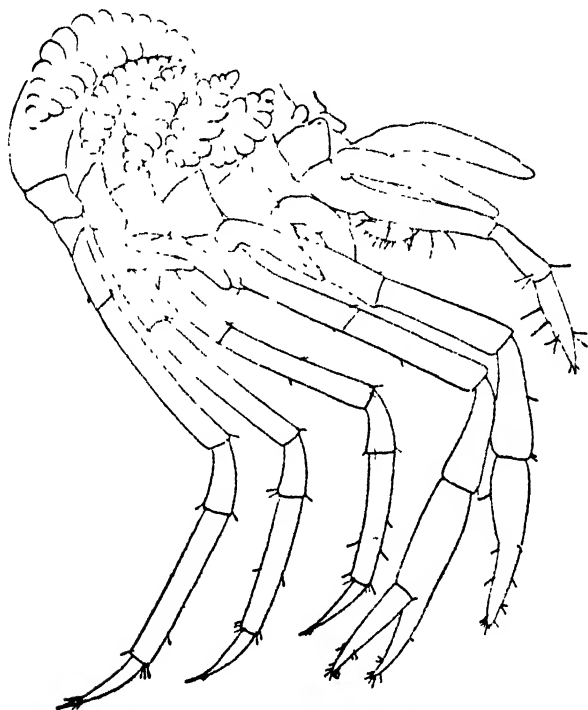
(6) 2nd antenna. Has the adult form, the scale having an outer terminal spine, and the flagellum very long, with about 17 joints. The basal joints of the peduncle and flagellum are arranged as in the adult. It is clear from a comparison with the larvæ that the apparently basal joint of the flagellum is actually a sclerite segmented off from the basipodite, and is not really an independent segment of the endopodite itself. The protopodite therefore consists of three and not of two segments,

but the third is a secondary acquisition. I can see no evidence that the peduncle is primarily three-jointed.

(7) The mouth-parts. The mandible and maxillæ have practically changed to the adult form, and the 2nd maxilla has lost entirely the lacinia of the coxopodite. (Text-fig. 10 B.)

The epipodite of the first maxillipede is a Y-shaped structure with two narrow arms, and has not acquired its final shape. The second maxillipede differs from that of the adult in several respects. The coxopodite bears only a small knob representing

Text-figure 8.

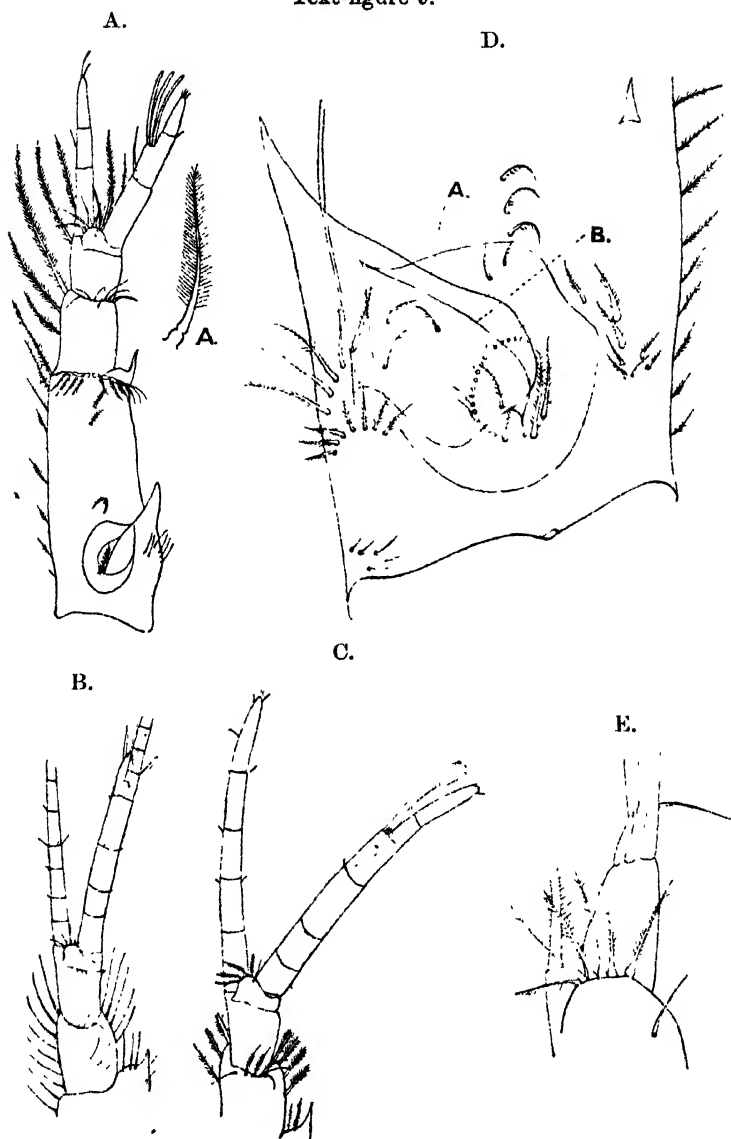


Thoracic appendages of first post-larval stage,  
showing gills and exopodites.

the future epipodite and podobranch, while the terminal joints of the endopodite are intermediate in form between that of the larva and of the adult. Curiously enough, the exopodite of the second and third maxillipede loses its setæ altogether at this stage and reacquires them at the next moult.

The third maxillipede has a small lobe on the coxopodite representing the epipodite, and a small knob may in some specimens be seen at the point of articulation which probably

Text-figure 9.

*Palæmonetes varians*. First antenna.

A. First post-larval stage.

B. Fifth post-larval.

C. Fourth post-larval.

E. Stage II. Showing antennular lobe and sensory setae.

D. Fifth post-larval—the otocyst.

A. Covering membrane of the stylocerite.

B. Edge of opening into otocyst.

represents the arthrobranch. The arthrobranch and pleurobranch are not developed till after two or three moults. Mortensen states that they do not appear in *L. fabricii* till the 9th moult (4th post-larval stage). In *P. varians* the pleurobranch is always very small and sometimes entirely absent. In one adult examined it was present on one side and absent on the other. Claus states that this gill is not developed in *P. varians*, but this is certainly not the case as a rule. (Text-fig. 10 C.)

(8) Pereiopods (text-fig. 8). Exopodites are always present on the first four pereiopods, generally, however, only as short rods without setæ. But there is much variation in this respect, and they are often, and particularly the fourth pair, found still to have setæ, though reduced in size. I shall deal below with the further development of the first two pairs of legs.

(9) Pleopods. These are now functional and provided with retinacula. No sexual differences are to be found in the second pair till the young prawn reaches a size of 15 mm., when a minute bud at the base of the retinaculum indicates the appearance of the *appendix masculina*. The appendix is not fully developed until the animal is nearly full-grown—20 mm. or more.

### Intermediate Post-larval Stages.

I have met with a few individuals in natural conditions, and with others reared in aquaria, in which the change from larval to post-larval form is effected through an intermediate stage combining the characters of both.

#### *Example 1. STAGE 5 C. (Text-fig. 11.)*

In this individual, taken at Blakeney, the characters of stage 5 B are retained for the most part, but the following features of the adult are acquired:—

(1) The rostrum has two dorsal and one ventral spine, the larval spines on the carapace being all retained.

(2) The chelæ of the first and second legs have nearly the post-larval form and arrangement of spines and setæ. The terminal long spine of the larva is lost from the second leg and retained on the dactylus of the first.

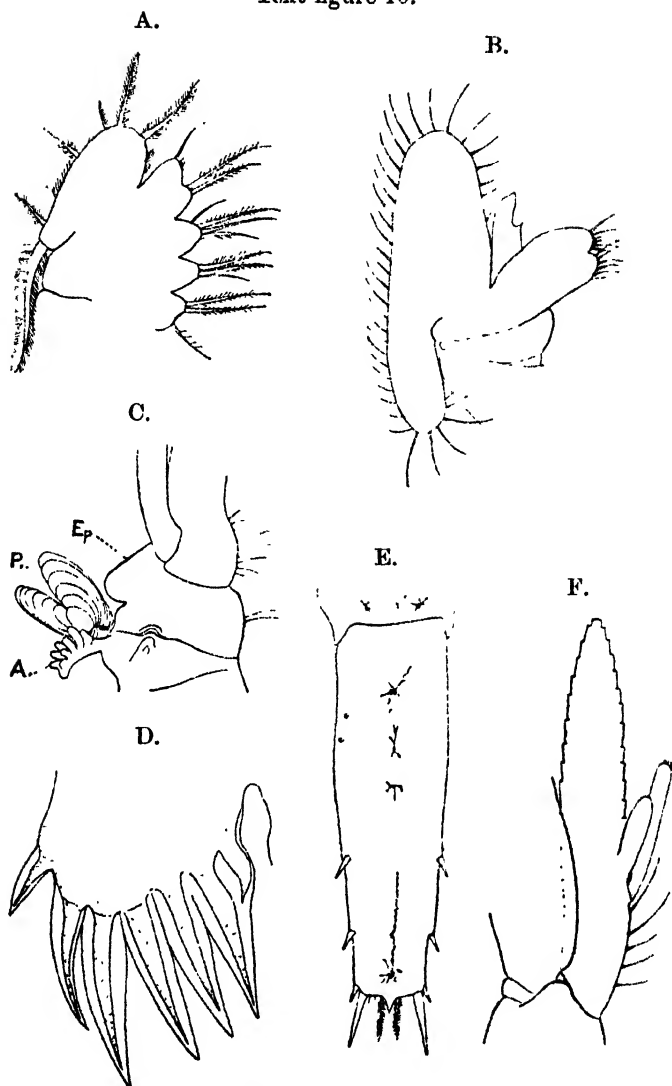
(3) The pleopods are setiferous and functional.

(4) The 1st antenna has the post-larval form.

The exopodites of the legs and the telson are as in the larva. In another very similar specimen from Blakeney the mouth-parts show rather more change, the endopodite of the second maxilliped in particular having acquired in part the post-larval structure and spines, without altogether losing the larval characters. The proximal lacinia of the 2nd maxilla is reduced, but is still present.



Text-figure 10.



A. 2nd maxilla. Stage I.

B. 2nd maxilla. First post-larval stage.

C. Basal joints of 3rd maxillipede. Adult of 33 mm. Ep, Epipodite.

A. Arthrobranch. P. Pleurobranch.

D. Telson of embryo removed from egg. Left half only shown.

E. Telson. Second post-larval stage.

F. 2nd pleopod. Young male of 18 mm.

Text-figure 11.

*Palæmonetes varians.*  
Stage V.C.*Example 2. STAGE 5 D.*

In this specimen the larval carapace spines are reduced, the supra-ocular spine having disappeared, but the rostrum has acquired no new spines.

The telson has the larval form, though it has lost the median pair of setæ.

The octocyst is formed, though widely open.

The exopodites of the legs are well-developed, while the first two pairs of legs have otherwise the adult form.

A second specimen had traces of all the larval carapace spines, but had in addition two minute dorsal and one ventral spine.

## POST-LARVAL GROWTH.

The changes which occur in the young prawn at the successive moults following the moults to the post-larval condition affect mainly the following characters:—

(1) 1st antenna. The length and number of joints in the outer flagellum.

(2) Length of the joints in the first two pairs of legs.

(3) Reduction of the exopodites of the legs.

(4) Shape of the epimera of the 5th abdominal somite.

(5) Form of the telson.

Each moult is accompanied by changes in respect of one or more of these characters, but the change is small and irregular so that it is impossible to recognize definite stages.

1. *1st Antenna.* (Text-fig. 9.)

In the adult the outer sensory flagellum is 70-80 per cent. of the length of the peduncle, and the basal or "fused" part is about 75 per cent. of the whole. The distal, unmodified, part greatly exceeds the length of the peduncle.

In the first post-larval stage the whole outer flagellum is less than half the length of the peduncle, and consists of 3, or rarely 4, joints, the second joint bearing a group of 4 *æsthetes* on an inner notch. This notch seems to represent a fixed point in the flagellum, and from it will later grow out the short accessory flagellum. Growth and increase in the number of joints takes place proximally and distally of this point, joints being added at the base of the flagellum to the sensory part and also distally beyond the notch in question, the latter joints being slender and tactile.

The second and third post-larval stages (1st and 2nd moults) remain much the same as the first, the whole flagellum consisting of 4 or 5 joints, a basal thick part of 3 and a distal slender part of 1 or 2 joints. At the third (text-fig. 9C) moult a minute tubercle may make its appearance in the notch of the 4th basal joint, representing the first appearance of the accessory flagellum, and this flagellum becomes definitely distinct at the 4th moult, while at the same time the distal slender part becomes greatly elongated. The three terminal *æsthetes* of the basal portion are carried forward on the new accessory flagellum, and the distal part of the notched joint becomes separated as the basal joint of the distal part. It is quite clear that the accessory flagellum is an outgrowth from the thickened part of the outer flagellum. It is usual to speak of the shorter ramus of the outer flagellum as being "fused" to the longer for a certain part of its length, but it is perfectly evident that this short flagellum has at no time been a separate branch from the peduncle, and is not in any sense fused to the outer

flagellum. It is, in fact, an accessory outgrowth of the latter, and it is correct to speak of the peduncle bearing an outer and an inner ramus, the former bearing in addition an accessory branch. For the purpose of specific description the ramus may be divided into —

- (a) Basal part.
- (b) Distal part.
- (c) Accessory flagellum.

The latter is a new acquisition peculiar to the Palaemonidæ and some Alpheidæ, while the distinction between basal and distal parts is a character shared with Pandalidæ and others.

The adult form of antenna with 15-18 basal joints and 5-7 joints in the accessory branch is not attained till very near maturity, or a length of 30-40 mm. in the female and about 25 mm. in the male.

## 2. Second pair of legs.

In the adult the dactylus of this pair is from two-fifths to one third of the length of the whole chela, while the chela is considerably shorter than the carpus. The carpus is always longer than the merus—in some cases nearly twice as long.

In early post-larval stages the proportional lengths of these joints are very different from those of the adult, as is shown in the accompanying table.

In the first post-larval stage the chela is relatively much longer

TABLE I.

Showing growth of the joints of the 2nd Leg in  
*Palaemonetes varians*.

		Length of animal.	Dactylus.	Chela.	Carpus.	Merus.
1st Post-larval Stage		6.7 mm.	100	209	100	115
2nd	"	6.9 "	"	220	132	150
3rd	"	7.3 "	"	189	141	130
5th	"	8.5 "	"	216	166	147
7th	"	10.90 "	"	242	215	200
8th	"	11.97 "	"	228	210	208
—	♀	13.5 "	"	228	256	216
—	♀	16 "	"	262	324	257
—	♀	44 "	"	300	373	300

than in the adult, and the dactylus is generally more than half as long as the chela. The carpus varies greatly in length, but is usually considerably shorter than the chela and is always much shorter than the merus. There is great individual variability in the first post-larval stage and still more in later stages, so that it is impossible to say at what stage the adult condition is assumed; but generally the chela remains longer than the carpus till at least the seventh moult, when the young prawn has attained a length of about 12 mm. The carpus, on the other hand, rapidly increases in length in proportion to the merus, which it exceeds by a small amount at the second and third moults. The actual proportions of the adult are probably not attained till maturity, but from about 14 mm. length the carpus exceeds in length both the chela and the merus, so complying with the proportions characteristic of the species.

Ortmann (Zool. Jahrb. Syst. v. 1891), in his "Revision of the genus *Palæmon*," has discussed the changes in the proportions of the joints of the chelipeds with growth; but his conclusions are entirely contrary to my own with regard to *Palæmonetes*, and he states that growth takes place chiefly in the chela itself, and that when the carpus in the young is shorter than the claw the difference becomes greater, while when it is longer the difference becomes less. Also that a carpus which is shorter in the young never reaches or exceeds its length in the adult. In the British *Leanders* and *P. varians* the carpus is always much shorter in the early post-larval stages than the chela, and the greatest growth takes place in this joint, which, in all except *L. serratus*, eventually equals or exceeds the merus and approximates to or exceeds the length of the chela.

### 3. *Exopodites of the pereopods.*

The condition of the exopodites of the pereopods in the first post-larval stage probably depends a good deal on the vigour of the larva, greater vigour leading to greater abbreviation of development; but the general rule appears to be that they are present in the first stage as functionless branches without setæ but of considerable size (text-fig. 8). Commonly that of the fourth leg retains three or four short setæ, while the remainder either lack setæ altogether or have minute terminal spinules.

At the next moult the exopodites are not entirely lost, but are still visible as small papillæ on the coxopodites. They disappear altogether at the second moult.

The first and second post-larval stages are definitely recognizable by the condition of the exopodites as a general rule, but there are exceptional cases of the full retention of the exopodites in the first post-larval stage, which probably do not then lose them altogether till later than the second moult.

#### 4. *Epimera of the 5th abdominal somite.*

In the last larval stage these epimera are produced into long, somewhat downcurved, pointed processes, and in the first post-larval stage these processes, though much reduced, are still as a rule retained. In the next moult they may be lost altogether, but very commonly a small point is retained, not only in the second stage, but up to the 5th moult and at a length of 11 mm.

#### *Rate of Growth and Maturity.*

At the moult from larval to post-larval the young prawn reaches a length of 7.76 mm. The first three moults are passed through at intervals of 4 or 5 days without any great increase of size. Intervals between moults become gradually longer, but are very variable in captivity—for instance, the intervals between the 3rd and 4th moult in five specimens were 5, 8, 8, 15.6 days, an average of 8.4 days. By the 8th stage (7th moult) a size of about 12 mm. is reached.

By August 10 the young prawns at Cley had reached a size of 12-16 mm., being then probably about two months old and having passed through nearly 10 moults. A month later, young of the year were found ranging from 16 mm. to about 24 mm., and the distinction between young and adults became difficult to draw except by examination of the antennule in the case of females and of the male appendix in the case of the males.

The first sign of the appendix is seen at a size of about 18 mm. (text-fig. 10 F), and below this size it is impossible to distinguish the sex either by this character or by the position of the legs. At 23 mm. the sexual characters are almost fully developed, the male appendix being of full size but without its full complement of setae. At 28 mm. the animal is completely developed.

#### *Development of the Otocyst.*

The first appearance of the "auditory" organ may be said to be traceable in the third larval stage, when a small notch is developed at the base of the antennules, in which are seated 3 or 4 short ciliated setae of the same type as are found later in the otocyst. In the fourth stage the projection of the antennules which bounds the notch and will eventually form the scaphocerite becomes larger, but there is no insinking of the stem to form an auditory vesicle. In stage 5 A the conditions are much the same, but in some, if not in all, specimens of 5 B there is an oblong pit completely open except where its proximal end is slightly overlapped by an extension of the scaphocerite.

The intermediate stage described above as 5 D shows a specially interesting condition, since the membranous overlap of the stylocerite has extended over a large part of the pit and the anterior side has also begun to close in.

In the first post-larval stage the auditory vesicle has attained to its final functional form, and contains grains of sand or other foreign bodies. In life there is generally a rather large slit-like opening into the vesicle, but in the moulted skin which it is convenient to use for study the stylocerite is usually displaced in such a way as to close this opening. In any case, it appears that the cavity is open to the exterior not only dorsally by means of this slit, but also laterally, since the stylocerite has the form of a membranous reduplication of the integument and is hollowed along the outer edge of the antennular shaft. In this way it forms, as it were, a tubular outer entrance to the broad dorsal opening of the vesicle (text-fig. 91).

The surface of the antennule in the neighbourhood of the otocyst is provided with numerous ciliated setæ of a sensory type.

For the most part the otocyst of young prawns reared in captivity has been found to be empty at all events in the first few stages, but this may be due simply to absence of suitable material.

The opening of the auditory sac beneath the outer fold of the stylocerite remains very large.

#### COMPARISON BETWEEN THE DEVELOPMENT OF *P. varians* and *P. vulgaris*.

The larval development of *P. vulgaris* has been fully described by Faxon (1879), so that it is possible to make a detailed comparison between the two species. The result is rather remarkable, since it appears that there is very little correspondence between the stages, and the larvæ differ in some respects from one another more than either does from the larva of the genus *Leander*.

- Stage I.—The larvæ of *P. varians* are larger at this and in all later stages than those of *P. vulgaris*. While the latter has only rudiments of the first two pairs of legs, *P. varians* has rudiments of all legs. Otherwise the structure is the same.
- Stage II.—*P. varians* has two pairs of swimming legs, while *P. vulgaris* has one only developed. In *P. varians* leg 5 is fully developed, gills are present, and pleopod buds appear; while in *P. vulgaris* the 5th leg, gills, and pleopods are absent. The two larvæ are in fact entirely different.
- Stage III.—*P. varians* has two dorsal teeth, and continues to the end to have one more than *P. vulgaris*. The latter has still only two legs and no trace of the 5th leg or of pleopods. *P. varians*, on the other hand, has all legs except the 4th developed and large pleopod buds.

Stage IV.—Legs 3 and 4 are small in *P. varians*, but they are still rudimentary in *P. vulgaris*. The latter is also less advanced in respect of the development of the pleopods, the flagellum of the 2nd antenna, and the basal part of the 1st antenna.

Stage V.—The 5th leg of *P. vulgaris* reaches now the same stage of development as it reached in the 3rd stage in *P. varians*. The flagellum of the antenna is much shorter, but the telson is narrower than in *P. varians*.

Stage VI. (or V. B).—The larva at this stage are less different, but the legs of *P. vulgaris* are hardly so far developed as those of *P. varians*. On the other hand, the pleopods bear setæ, which is not the case in the latter until the post-larval stage.

It is clear that the evidence to be drawn from the larvæ is strongly against the validity of the genus *Palæmonetes*, which, indeed, can be separated from *Leander* only by the absence from the adult of the mandible palp. The absence of this palp alone is quite insufficient basis for the separation of the genus, since other *Palæmonidæ* have been discovered in recent years which lack a palp, but are in other respects quite obviously not members of the genus *Palæmonetes* (e.g. *Palæmonetes natalis* Stebbing, *Palæmonopsis* Borradaile). The absence of the palp is simply the retention of a larval character in the adult. Representatives of the genus occur in fresh or brackish water in widely-separated localities over nearly the whole world, but it seems to be not at all improbable that the species may have originated independently from distinct forms of the genus *Leander* in adaptation to new conditions in much the same way as *Limnocalanus macrurus* has been independently derived from *L. grimaldii* not only in America, England, and Scandinavia, but even in several of the lakes in Sweden\*. If this is true, it may none the less be a matter of convenience to retain the genus as an artificial group of species having distinct similarity of habitat and a single distinguishing character rather than to merge them all into *Leander*, which is already a somewhat unwieldy and ill-defined group.

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\* Gurney, Proc. Linn. Soc. xxxv. p. 431, 1923. Ekman, Int. Rev. Ges. Hydrol. Hydrol. vi. p. 335 (1913).



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## EXHIBITIONS AND NOTICES.

February 5th, 1924.

Sir SIDNEY F. HARMER, K.B.E., F.R.S., Vice-President,  
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the months of November and December, 1923 :—

## NOVEMBER.

The registered additions to the Society's Menagerie during the month of November were 93 in number. Of these 44 were acquired by presentation, 16 were deposited, 19 were purchased, 11 were received in exchange, and 3 were born in the Menagerie.

The following may be specially mentioned :—

1 Young Pigmy Hippopotamus (*Cheropsis liberiensis*), from Liberia, purchased on November 2nd.

1 Young Walrus (*Odobenus rosmarus*), from Norway, purchased on November 19th.

1 Grant's Zebra (*Equus quagga granti*), from Tanganyika Territory, presented by W. T. H. Hilpern on November 5th.

1 Sable Antelope (*Hippotragus niger*), presented by the Lord Queensborough on November 23rd.

A collection of Antelopes from South Africa, purchased on November 23rd, consisting of 2 Sable Antelopes (*Hippotragus niger*), 2 Water-Bucks (*Cobus ellipsiprymnus*), and 1 Brindled Gnu (*Gorgon taurinus*).

## DECEMBER.

The registered additions to the Society's Menagerie during the month of December were 208 in number. Of these 16 were acquired by presentation, 129 were deposited, 36 were purchased, 17 were received in exchange, and 10 were born in the Menagerie.

The following may be specially mentioned :—

1 Chimpanzee (*Anthropopithecus troglodytes*), from West Africa, purchased on December 21st.

2 Jerboa Rats (*Notomys mitchelli*), from New South Wales, new to the Collection, purchased on December 19th.

2 Red-breasted Parrots (*Perocephalus rufiventris*), from Abyssinia, new to the Collection, purchased on December 19th.

4 Cayenne Crakes (*Creciscus cayennensis*), from Brazil, new to the Collection, deposited on December 27th.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a series of photographs of Zebras.

The SECRETARY exhibited, and made remarks upon, some photographs of a Chimpanzee and its "nest."

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a piece of ship's timber attacked by Marine Boring Animals.

### February 19th, 1924.

Prof. J. P. HILL, F.R.S., Vice-President,  
in the Chair.

The SECRETARY read the following Report on the Additions made to the Society's Menagerie during the month of January, 1924 :—

The registered additions to the Society's Menagerie during the month of January were 133 in number. Of these 33 were acquired by presentation, 15 were deposited, 39 were purchased, 26 were received in exchange, and 20 were born in the Menagerie.

The following may be specially mentioned :—

1 Madras Langur (*Presbytis priamus*), from South India, received in exchange on January 5th.

1 African Ratel (*Mellivora ratel*) and 1 Ethiopian Ant-Bear (*Orycteropus aethiopicus*), from Abyssinia, received in exchange on January 25th.

4 Blue-naped Colies (*Colinus macrurus*) and 3 Pigmy Falcons (*Polichierax semitorquatus*), from Abyssinia, new to the Collection, received in exchange on January 29th.

### A NEW GENUS OF MONKEYS.

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited a series of lantern-slides to illustrate the characters of a new genus of Monkeys, *Presbytiscus*, founded upon the species described by Dollman as *Rhinopithecus avunculus* (Abstr. P.Z.S. 1912, p. 18). *Presbytiscus* resembles *Rhinopithecus* in cranial and facial characters, having a small upturned nose and a long upper lip, thus differing from *Nasalis*; but it differs from *Rhinopithecus* in the structure of the hands and feet, which have digits remarkably long, as in *Nasalis*, the tip of the hallux, when turned forwards, reaching to the

distal end of the first phalange of the 2nd digit. In *Rhinopithecus*, as in the Langurs (*Pithecus*), the digits are much shorter, the hallux, when turned forwards, not extending so far as the distal margin of the plantar pad.

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Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a series of Cinematograph films taken in the Society's Gardens.

**March 4th, 1924.**

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

Dr. D. H. HUTCHINSON, exhibited, and made remarks upon, a series of Cinematograph films of the movements of *Amoeba*, *Volvox*, *Vorticella*, *Paramecium*, *Plumatella*, and embryo Herrings.

Mr. H. C. BROOKE exhibited, and made remarks upon, a specimen of a "Blue" coloured *Rattus rattus*.



15. The Atmospheric Conditions at the Zoological Gardens, London. By LEONARD HILL, M.B. (Lond.), F.R.S. (From the National Institute for Medical Research, Hampstead, N.W. 3.) \*

[Received January 8, 1924: Read March 18, 1924]

A great deal of evidence has been gathered in recent years showing the benefit of exposure to sunshine and open-air. Children have been cured of surgical tuberculosis by proper splinting, good feeding, and exposure, under Bernhardt and Rollier in the Alps, and Gauvain at the Treloar Hospital, Alton, in England.

Many have followed these pioneers in carrying out this treatment in different countries. Children are stripped and exposed on open galleries in suitable weather and become hardy and brown as negroes. Argyll Campbell and Leonard Hill have shown that their metabolism when at rest is put up some 50 and even 100 per cent. and their appetite thus improved; their muscles become hard and they themselves happy even when splinted and at rest in bed. It has been shown, moreover, that the rickety changes produced in young animals, and children, by diet ample in energy value but deficient in antirachitic substances, are prevented, or cured, by exposure to ultra-violet rays whether of the sun, carbon arc, or mercury vapour lamp (Huldschinsky, Hess, Chick, and others). Young rats, moreover, when fed on a diet ample in energy value but deficient in a principle necessary for growth, viz., the fat soluble vitamin A, survive longer when exposed day after day in a suitable climate to sunshine and open-air, and their resistance to infection being so increased they show far less of that inflammation of the eye and ear which is a characteristic result of this deficiency of diet, and all this in spite of ceasing to put on weight (Park, Powers, and Symonds).

In Vienna, children fed on a deficient diet after the War were treated in hospital in two lots—one in the ward under glass and the other out-of-doors in the sunlight. Of the first lot, all showed, on X-ray examination, signs of rickets, while all of the second lot were free from rickets (Chick). Experience gained at open-air schools shows the great benefit resulting therefrom. Delicate children suffering from chronic catarrh, nervous children, those with some trouble or poor appetite and digestive weakness, there alike become strong and healthy.

While in New York there are over 120 such schools, in London there are but two or three. Smoke-pollution cuts down the light of the cities and intensifies the effect of confinement indoors and overclothing. In the Zoo there are many animals kept under glass

\* Communicated by the SECRETARY.

which have no access to the open air and sunlight. The shorter ultra violet rays present in high sunlight, which have a powerful action on the skin, are cut off by window-glass. These animals are in this respect even worse off than children who sometimes get out into the streets. While rickets is a disease produced by bad feeding and darkness, tuberculosis is a disease of domesticity, most prevalent in crowded, ill-ventilated, over-warm dwellings. While well-fed animals do not become rickety, even when kept in the dark, ill-fed animals can be protected from rickets by exposure to ultra-violet rays. It should, then, be a general rule to give animals kept in captivity access to the open-air, so that they can easily go in and out according to their own instinct. While there is no advantage in going outside in smoke-fogs, in dark weather there would be advantage in occasionally giving animals baths of radiant energy from arc-lamps. It has been proved that such baths have a curative effect in cases of surgical tuberculosis as well as of rickets. It has been shown that wounds heal well when the wounded are treated in open verandahs; the wounds are benefited when given light-treatment.

L. Colebrook, A. Eidinow, and Leonard Hill have found that the bactericidal power of the blood is put up to a significant extent shortly after an exposure of animals to ultra-violet rays. To get this effect the animals are shaved over an area and this area so exposed that erythema results.

As stated above, young rats on a diet deficient in vitamine A live longer and suffer less from infection when exposed to summer sun and open-air in a genial fine-weather climate. Ultra-violet and light rays produce a flushing of the skin and increased exudation of lymph followed by desquamation and pigmentation. The last cannot take place in albinos, and such withstand exposure to the strong sun badly. White-furred animals are not necessarily albinos, many have pigmented skins beneath their fur and are most suitable for living in tropical climate, as the white fur reflects and scatters light and the pigment prevents the blood and subcutaneous tissues being hurt by the rays which otherwise would penetrate to them in excess. Light acts on the naked parts of the faces of furry animals, *e.g.*, the lips, nostrils, conjunctiva, ears. The effect of light is mitigated and controlled by cutaneous pigment. Thick hides, such as that of the elephant, must be unaffected by light, excepting a possible sterilizing effect acting on the very surface. While ultra-violet rays have very little penetrating power and are absorbed by the outer layer of the skin, visible rays penetrate to the subcutaneous blood-vessels of thin-skinned animals such as man, and warming up the blood locally have a beneficial effect.

While the skin is exposed to the insults of the world and has the power of resisting microbic invasion, adequate stimulation of the skin by sunlight is of great importance in keeping up this immunity. In the cases of rickets, exposure of the skin to the

action of the ultra-violet rays stimulates better absorption of salts of calcium and phosphorus from the bowels, probably by limiting microbial fermentation therein.

Just as children with lupus are exposed naked to a large carbon arc, sitting in a circle round it, so small animals might have a circular arrangement of cage with an arc in the middle, a circular path being arranged for visitors outside; to give red radiant heat in place of dark heat from hot-water pipes, a circular gas-fire might be placed in the middle, but the arc is best. Then, with the animals warmed by radiant energy, an adequate circulation of cool air could be maintained through their houses. Radiant energy, which penetrates to, and warms up, the subcutaneous blood, is better than dark heat which warms the surface of the skin. The use of hot-water pipes, although economical, entails a low ventilation rate and stuffy warm-air conditions which increase catarrhal infection and pneumonia.

The breathing of cool air has a most important effect in keeping up the defence of the respiratory membrane against catarrhal infections and tuberculosis. The exhaled air is warmed up almost to body-temperature and saturated with moisture. It holds about 40 gm. of water per cubic metre. Air at 0° C. holds, when saturated, only 5 gm. of water. Thus every cubic metre breathed of such cold air takes away 35 gm. of water. Warm moist air takes away half or less this amount. The warming and saturating of cool air entails a rapid flow of blood lymph and secretion through the respiratory membrane, and this keeps it clean and in cool condition. Catarrh and pneumonia are spread, not by exposure to cold, for Arctic travellers and such-like exposed to extremes of cold—hunters and open-air workers—do not suffer, but to crowding in stagnant warm humid atmospheres where infection from mouth and nose of carriers of catarrhal complaints is massive. Experience at sanatoria shows that when bad weather confines patients within doors at the time of visitation of an influenza epidemic, more chest complications occur than when, under such visitation, they are out of doors. All cases of pneumonia and acute fever, the wounded, and mental cases do much better treated in open-air verandahs than in hospital wards.

Exposure to the cooling power of the open-air, while raising the basal metabolism, excites muscular exercise, deeper breathing, a better circulation, more active digestion and appetite, and prevents constipation. It thus promotes general good health. At the same time, exposure must not be excessive or go beyond the power of the animal to keep warm by increased body-heat production. Big animals, owing to their large bulk and relatively small surface-exposure, withstand exposure to cold, while small warm-blooded animals have to seek the protection of nests and live a communal life, keeping each other warm in clusters. Thus, three or four pregnant tame mice, kept in the same box, will make a common nest and fill it with two or three dozen young mice, which probably share in a communal milk-supply. Rats on a cold day



because of the full exposure to wind. Thus the mean monthly range near the ground in a sheltered court in London was  $5\frac{1}{2}$ –10 against 21–40 on the top of Kew Observatory. Most animals shelter themselves from wind and get into lairs at night. The cooling powers to which they are naturally exposed are then much lower than the above. The following readings, taken during the day in various parts of the world, show what is more like the range to which most animals are exposed at times. Sea-birds and Arctic and mountain warm-blooded animals are exposed to very high cooling-powers.

As will be seen on consulting the tables given below in the Appendix, low cooling-powers and general monotony of conditions are noticeable at the Zoo in the small birds' house, the reptile house, the apes' house, and the hippopotamus house; the readings closely resemble those found in many factories which are kept over-warm, stagnant, and monotonous.

During March, April, and May the water-pipes were heated in the antelope house, and yet the cooling powers and temperatures were about the same as in the deer and cattle sheds which were unheated. The suggestion arises, therefore, that the artificial heat was wasted and might be discontinued—at any rate, during such a period as that observed.

The range of cooling-powers is much too low in the Sanatorium and Operating Theatre at the Zoo.

The suggestions made, as the result of this enquiry, are (1) that radiant heat and cool air might be tried in preference to the present plan of heating air and making it humid and monotonous by shutting up houses and heating with hot-water pipes; (2) that animals from warm countries have, as far as possible, choice given them of going in and out of the open-air. This has already been given with success, so the Superintendent tells me, in the case of some of the higher apes.

The author is indebted to Miss M. Brad for her careful taking of readings and to Drs. Chalmers Mitchell and Vevers for making the enquiry possible by their kind co-operation.

## APPENDIX.

### ENGLAND.

*Hull. Jan. to June, out-of-doors 9 A.M.*

	Cooling Power.		Temperature ° F.	
	Dry kata.	Wet kata.	Dry bulb.	Wet bulb.
Warm, bright ..	7-12	22-34	55-66	50-59
Cool, bright . . .	15-21	28-41	49-60	42-46
Cold and bracing ..	14-23	32-49	42-44	37-42
Cold ....	25-31	53-61	38-47	35-43

# EGYPT.

## Cairo.

	Cooling Power.		Temperature ° F.	
	Dry kata.	Wet kata.	Dry bulb.	Wet bulb.
Close and oppressive	1½-5	11-16½	70-90	65-78
Cool . . .	6-9	11-24	58-62	51-57
Hot windy . .	3-0	24-34	91-95	58-65

On close days, low dry and wet kata readings and so heat loss by convection and evaporation difficult.

# CEYLON.

## September.

	Cooling Power.		Temperature ° F.	
	Dry kata.	Wet kata.	Dry bulb.	Wet bulb.
On a verandah . .	1-2	25-32	81-89	77-79

As in Cane on hot windy days, very low dry but high wet kata readings, so heat loss by evaporation easy.

# INDIA.

*Lahore.* Open readings taken under a meteorological conical roof at 16.00 hrs. for year 1921. The free vertical movement of air was confined by roof.

Months.	Cooling Power.		Temp. (Mean) ° F.		Wind-velocity. m.p.h. (1872-1920.)
	Dry kata.	Wet kata.	Dry bulb.	Wet bulb.	
Dec., Jan., Feb.	7.1-8.9	24.1-25.6	69.0-75.7	55.3-60.0	0.9-1.6
Mar., April, May, June.	* -2.3-1.4	12.7-26.4	80.4-108.9	64.9-81.7	1.5-2.6
July, Aug., Sept.					
Oct., Nov.	2.1-4.6	17.7-18.7	80.3-88.9	61.0-70.5	0.9-1.1

# AUSTRALIA.

*Jerilderie.* { 210 miles inland from South Coast of Australia.  
                  { 420 " " " East " "

628 feet above sea-level, within 40 yards from Billalong Creek; extensive plains with belts of timber here and there.

Months.	No. of Obs.	Cooling Power.		Temperature ° F.		Wind-velocity. m.p.h.
		Dry kata.	Wet kata.	Dry bulb.	Wet bulb.	
Sept.	5	10.0-15.5	20.9-28.4	53-64½	44-53½	2.0-2.6
Oct.	2	8.8-17.0	23.5-35.6	53-65	40-53½	1.18-3.0
Nov.	2	4.3-9.7	18.6-39.2	76-80½	53½-65	1.0-4.9

\* The - sign signifies that the dry kata had to be cooled below 95° F., and its rate of warming up from 95-100° F. was determined in hot weather instead of its rate of cooling down.

## CALIFORNIA.

*Burlingame, 9 A.M.*

Months.	Cooling Power.		Temp. ° F. Dry bulb.	Wind-velocity. m.p.h.
	Dry kata.	Wet kata.		
Aug., Sept., Oct. } Nov., Dec., 1922. }	8.1 12.0	20.2-21.2	44½-61½	5-9
Jan., Feb., Mar., 1923.	13.8-14.6	25.1-25.5	30-52½	0-1.7

## BRITISH COLUMBIA.

*East Kelowna, 9 A.M.*

Months.	Cooling Power.		Temp. ° F. Dry bulb.	Wind-velocity. m.p.h.
	Dry kata.	Wet kata.		
Aug., Sept., 1922.	6.2-6.3	19.8-21.3	62½-65	0.2-0.3
Dec. 1922, Jan., Feb., } Mar., Apr., 1923. }	12.5-15.5	25.7-30.1	34-57	0.6-1.7

## SOUTH AFRICA.

*Johannesburg.*

On a day in	Cooling Power.		Temp. ° F. Dry bulb.
	Dry kata.	Wet kata.	
Feb., Mar., April, June, } Oct., Nov., Dec., Jan. }	0-17	28½-51	51-75
July	23	45	45

## BALKANS.

	Cooling Power.		Temperature ° F.
	Dry kata.	Wet kata.	
Hot weather	3-4½		77-86
Pleasantly warm	5-8		67-84
Pleasantly cool	8-12		67-73
Chilly	12-14		57-67
Raw, chilly	11-20		32-52
Sunny, cool, bracing	10½-18½		25-44½
Very cold	23-39		30-41

## SWITZERLAND.

*Davos.*

	Cooling Power.		Temperature ° C. Dry bulb.	Wind-velocity. m.p.h.
	Dry kata.	Wet kata.		
January	22	40	-5.6	1.1
March	22	44	1.4	3.1
May . . . . .	19	39	9.6	3.4
July	15	37	14.0	3.0
Sept. . . . .	17	38	11.0	3.0
Nov. . . . .	21	41	-2.3	1.6

# FACTORIES, etc.

Taken from thousands of readings.

## SOUTH AFRICA.

### *Johannesburg.* White Theatres and Cinema Halls.

	Cooling Power.		Temperature ° F.		Wind-velocity. m.p.h.
	Dry kata.	Wet kata.	Dry bulb.	Wet bulb.	
March 5-15, 1921 ...	4-6	14-22	67-76	—	—

### *Natal.*

Jan. and Feb.					
Inside	1-5	12-23	80-92	70-78	--
Outside	4-12	19-33	70-86	64-76	—

### *Rand Mines.*

* Working places	2-5	8-19	65-87	61-86	—
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## ENGLAND.

### *Boot and Shoe Factories.*

Winter and Summer. Mean observations	6-7	17-21	59-67	—	0.3-0.5
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### *Printing Works*

Jan.-April	5-9	16-23	55-72		0.1-0.6
June-July, warm weather	1-6	13-19	67-84	--	0.1-1.5

### *Cotton-Weaving Sheds.*

Mean Observations.					
Winter	4-5	13-18	65-74	62-71	0.3-0.4
Summer	4-5	12-17	72-77	63-73	0.2-0.5

### *Laundries.*

Hand-ironing room	2-7	—	69-89	-	0.2-1.6
Calender-room	1½-5	—	70-83	—	0.1-4.7

### *Large Steamers on American Route.*

Dynamo-room	0-7	14-28	77-103	65-81	0.9-2.3
3rd Class Cabins	4-5	12-16	73	66-67	0.0-0.3

Stagnant over-warm conditions.

\* Working efficiency of natives in places with lowest cooling-power 50 per cent below that in places with highest cooling-power.

# IN OPEN AIR, ZOOLOGICAL GARDENS, LONDON, 1923.

Month.	No. of Obs.	Cooling Power.		Temperature ° F.		Black Fur, ° F.
		Dry kata.	Wet kata.	Dry bulb.	Wet bulb.	
March	3	10.4-18.0	30.4-37.8	52.0-68.0	50-59.8	62.7-86.7
April	14	9.4-23.7	25.1-46.3	43.0-68.0	40.2-60.8	50.0-82.5
May	5	5.5-15.3	22.7-32.6	60.8-77.0	52.7-66.3	67.7-90
June	1	6.3	23.6	75.2	64.5	118.4
August	6	4.6-8.8	17.2-31.3	75.2-84.2	64.5-70	83.4-99.5

## SMALL BIRDS' HOUSE.

Month.	No. of Obs.	Cooling Power.		Temperature ° F.		Black Fur, ° F.	Wind- velocity, m.p.h.
		Dry kata.	Wet kata.	Dry bulb.	Wet bulb.		
March	3	6.6-6.9	18.1-21.6	68.0-70.0	58.1-59.8	70.0-72.4	0.6-0.9
April	11	5.6-7.7	15.8-23.5	57.3-68.0	51.0-62.7	59.7-71.7	0.2-0.8
May	5	4.9-7.6	14.0-19.5	64.5-76.2	58.1-66.3	66.3-79.0	0.3-0.7
June	2	4.8	14.8-15.4	71.7-72.5	62.7-63.5	75.2-77.8	0.2-0.3
August	6	4.1-6.3	15.1-17.5	71.7-80.7	62.7-66.3	75.2-82.5	0.3-1.0

## REPTILE HOUSE.

March	2	5.5-5.9	16.5-17.3	68.0	59.8-60.8	70.0	0.2-0.4
April	9	4.9-6.5	14.5-19.0	66.3-70.7	56.4-64.4	68.0-75.5	0.2-0.5
May	4	3.7-5.0	14.3-19.6	71.7-79.0	60.8-68.0	73.8-83.4	0.3-0.7
June	2	3.7-5.3	14.4-18.7	75.2-79.7	64.5-68.0	77.4-81.5	0.4-0.7
August	7	2.4-4.9	12.0-16.4	77.0-86.0	65.4-73.0	81.0-89.7	0.2-0.7

## ATE HOUSE.

(Hot-water pipes with troughs of water on them.)

March	2	6.0-6.1	17.4-18.9	68.0	59.0	64.5-68.0	0.3-0.4
April	13	4.8-8.2	17.7-23.2	64.3-71.6	53.8-62.8	65.3-73.5	0.2-1.0
May	4	4.1-7.0	17.3-19.8	66.3-77.0	57.3-65.3	68.0-79.5	0.3-0.6
June	1	4.4	15.9	75.2	63.5	73.5	0.3
July	5	3.4-5.3	13.0-15.4	71.6-80.7	66.3-70.7	77.0-83.3	0.2-0.5

## HIPPOPOTAMUS HOUSE.

(Heated by hot-water pipes.)

March	1	7.1	18.7	64.5	55.5	63.3	0.5
April	12	6.2-8.5	15.5-22.5	55.5-64.0	50.0-60.8	57.3-63.3	0.1-0.4
May	4	4.5-8.3	16.5-22.0	60.8-76.2	53.7-66.3	62.7-79.0	0.4-0.9
June	1	5.0	14.8	71.6	62.7	74.5	0.3
August	6	3.3-5.4	12.7-17.0	75.2-82.5	64.5-70.7	75.2-85.0	0.1-0.6

## ANTELOPE HOUSE.

(Heated; open to paddock.)

Month.	No. of Obs.	Cooling Power.		Temperature °F.		Black Fur, °F.	Wind-velocity, m.p.h.
		Dry kata.	Wet kata.	Dry bulb.	Wet bulb.		
March	1	9.2	23.5	64.0	52.0	62.1	1.1
April	6	8.6-12.2	17.7-31.0	50.6-64.5	44.7-59.0	52.0-58.3	0.5-1.4
May	3	5.3-9.3	21.9-26.3	61.5-77.8	56.4-66.3	66.3-79.2	1.1-1.8
June	2	4.5-6.5	14.9-19.7	68.0-73.5	59.0-62.7	70.8-76.7	0.3-0.5
August	6	3.5-7.2	14.1-23.6	73.5-85.2	61.5-70.3	75.2-88.0	0.4-1.5

## DEER AND CATTLE SHEDS.

(Open to paddock; no artificial heat.)

April	6	7.9-12.3	18.8-24.7	46.4-57.3	41.0-52.0	48.2-60.8	0.3-1.1
May	5	7.0-9.5	20.0-22.1	61.0-79.0	54.5-65.3	64.3-80.7	0.8-2.9
June	1	5.1	19.4	73.4	64.5	78.0	0.5
August	7	2.7-6.4	13.8-20.1	73.4-86.0	62.7-71.7	79.0-89.7	0.5-1.4

## RANGES OF FIGURES IN VARIOUS OTHER HOUSES.

March, April, May, June, and August.

House.	No. of Obs.	Cooling Power.		Temperature °F.		Wind-velocity, m.p.h.	
		Dry kata.	Wet kata.	Dry bulb.	Wet bulb.		
Monkey }	16 {	6.5	18-23	57-66	50-59	0.2-0.6	{ Cool weather. Warm weather.
" }		3½-5	13-17½	68-90	61-71		
Tortoise	7	4-7	14-20	64½-75	60-66	0.3-0.7	Cool weather.
Lion }	10 {	4.8	14-22	59-79	52-57	0.3-1.0	On one occasion
" }		13	25	52	40½		
Parrot	5	6.8½	16½-20	52½-70	48-61	0.2-0.6	
Insect	16	4-7½	11-18½	61-75	52-66	0.1-0.6	
Small Mammal.	10	4-9½	15-22½	50-75	46-69	0.2-0.6	
Small Cat-house	12	14-11	15-27½	55-73½	50-62½	0.3-1.8	
Elephant	15	5-9½	16-24	56-72	46½-65½	0.2-0.7	
Rodent	12	3-7½	11-20	57-81	51-70	0.1-0.6	
Sanatorium	11	2-6	12-16	68-90	57-70	0.1-0.8	
Operating theatre	4	2½-4	13-16	69-82	56-71	0.1	
Small birds' (outside cage).	26	5½-20½	21-37	46½-80½	39-67	0.1-3.2	



16. Nomina Conservanda in Mammalia. By OLDFIELD THOMAS, F.R.S., F.Z.S., and other European Mammalogists.

[Received February 13, 1924: Read April 1, 1924.]

For various reasons the list of proposed Nomina Conservanda in Mammalia, published in the 'Zoologischer Anzeiger' for 1914\*, and submitted formally to the Nomenclature Commission in Washington, has never been adjudicated upon. The names, therefore, remain more or less in doubt, to the very great inconvenience of working mammalogists, although the inconvenience has been modified by a fairly general agreement that until judgment is given the "Fiat" names shall continue to be used.

It appears to us, however, that it would now be a great practical convenience to mammalogists in general if the names were again to be published in some such well-known periodical as the 'Proceedings of the Zoological Society,' where they would be readily accessible to all workers.

We are unanimously agreed as to the advantage to be gained by the fixing of these names, every one of which has been most carefully considered, and we hope that in due course they will be formally accepted by the Commission. Full reasons for the use of them have been submitted to the Commission, and need not here be repeated, especially as they are widely known to all mammalogists. But a brief note on each is appended.

We now therefore publish the following list of them, and desire to express our intention of continuing to use them whenever occasion may arise.

1. ANTHROPOTHECUS.

To be used for the Chimpanzees instead of *Simia* or *Pan*, whose application to these animals is quite unknown to most naturalists. Genotype: *A. niger* Geoff.

2. CERCOPITHECUS.

For the "Guenon" monkeys of Africa, with genotype *Simia mona* Schr.

The attempt to use *Cercopithecus* for the Tamarins depends only on Gronovius, a doubtfully binomial writer, and it forms a transfer case of the very worst type.



## 3. CHIROMYS.

For the Aye-Aye. Genotype: *Sciurus madagascariensis* Gmel.

*Daubentonia*, which has priority, is almost unknown to general writers, to whom this morphologically interesting animal is always known as *Chiromys*.

## 4. CÆLOGENYS.

For the Paca. Genotype: *Mus paca* Linn.

*Agouti* and *Cuniculus* have been applied to the Paca, but both names are known, either as vernacular or technical terms, in connection with other animals, and the use of either of them for the Paca is most confusing.

## 5. DASYPUS.

For the 6-banded Armadillo and its allies. Genotype: *Dasypus sexcinctus* Linn.

By strict law *Dasypus*, which has been invariably applied to the true Armadillos, should be shifted to the Tatous (*Tatu*), a most confusing and objectionable transfer.

## 6. DICOTYLES.

For the Peccaries. Genotype: *Sus tajacu* Linn.

*Tayassu* is scarcely known, and its genotype by no means absolutely certain. Much confusion has arisen from the use of this name, and the well-known term *Dicotyles* should be retained.

## 7. ECHIDNA.

For the Spiny Anteater of Australia. Genotype: *Myrmecophaga aculeata* Shaw.

So universally known as the name for the Spiny Monotreme that any attempt to get *Tachyglossus* used by general writers is doomed to failure. *Echidna* would have to be withdrawn from Ichthyology, but workers in that group state that this would cause no difficulty or confusion.

## 8. GALEOPITHECUS.

For the Philippine Flying Lemur. Genotype: *Lemur volans* Linn.

*Cynocephalus* is technically applicable to the Flying Lemur, a particularly objectionable transfer of a name well known in connection with the Baboon's.

## 9. GAZELLA.

For the Gazelles. Genotype: *Gazella dorcas* Linn.

10. HAPALE.

For the true Marmosets. Genotype: *Simia jacchus* Linn.  
The transfer of *Callithrix* from the Titi Monkeys (*Calli-  
cebus*) to the Marmosets is highly confusing, and that name  
should be discarded altogether.

11. HIPPOTRAGUS.

For the Sable Antelope and its allies. Genotype: *Antilope  
leucophaea* Pall.

The wholly unknown name *Ozanna* has technical priority  
over the familiar *Hippotragus*, which should be retained.

12. LAGIDIUM.

For the Mountain Chinchillas. Genotype: *Lagidium  
peruanum* Meyen.

Instead of *Vizcaccia*, which, being the well-known ver-  
nacular name of the Argentine *Lagostomus*, is most unsuit-  
able.

13. MANATUS.

For the Manatees. Genotype: *Trichechus manatus* Linn.

The use of *Manatus* for the Manatees is familiar to all  
zoologists, while the transfer of *Trichechus* from the Walrus  
to these animals is most objectionable.

14. NYCTERIS.

For the African Bats usually so called. Genotype: *Vesper-  
tilio hispidus* Schr.

Technically *Nycteris*, well known for these African bats,  
would have to be transferred to certain American bats  
commonly known as *Lasiurus*. This transfer also affects the  
Family name Nycteridae.

15. RHYTINA.

For Steller's Sea-Cow. Genotype: *Manati gigas* Zimm.

The priority name *Hydrodamalis* is almost unknown to  
writers of any class.

16. SIMIA.

For the Orangs. Genotype: *Simia satyrus* Auct. nec  
Linn.

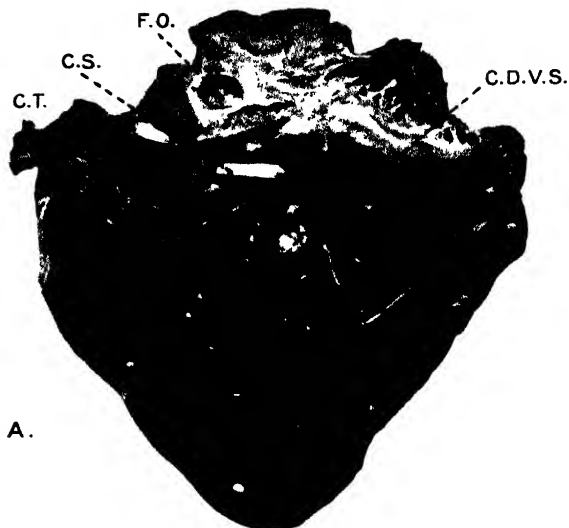
Specific name *satyrus* to be fixed as well as generic, the  
original *Simia satyrus* Linn. being a Chimpanzee.

The objectionable name *Pongo* is the technical alternative  
for the widely, indeed universally, used *Simia*.

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\* The original list was also signed by Knud Andersen and R. Lydekker, whose authority may also be quoted.





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A.



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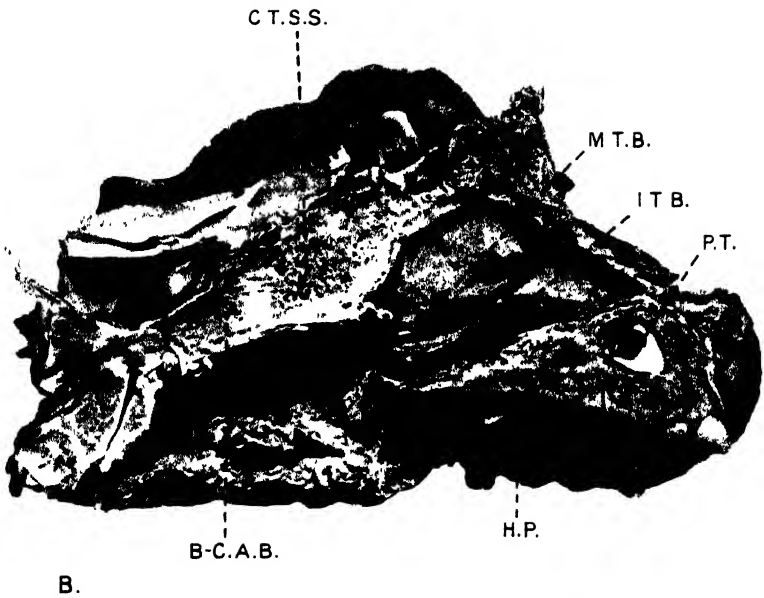
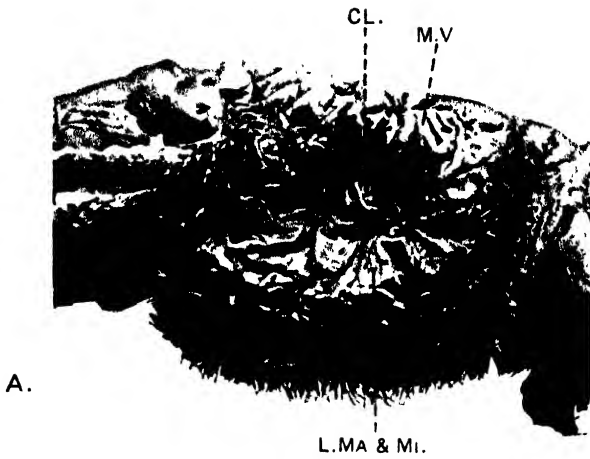


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ANATOMY OF THE ORANG - OUTAN.

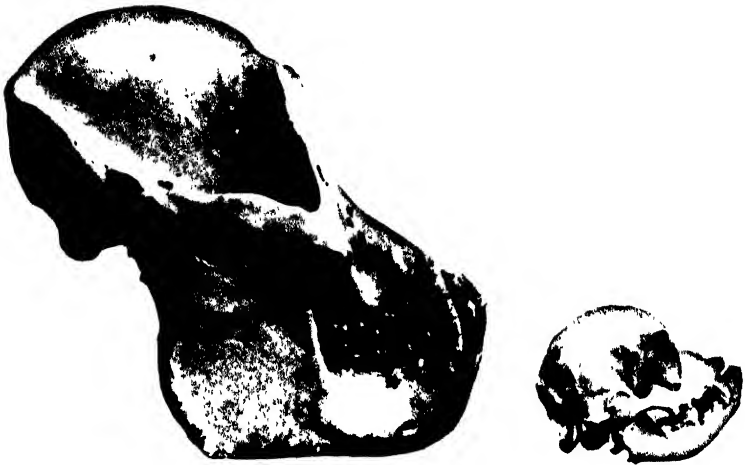






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A.



B.

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17. On the Anatomy, Physiology, and Pathology of the Orang-Outan. By CHARLES F. SONNTAG, M.D., Ch.B., Anatomist to the Society, and Demonstrator of Anatomy, University College.

[Received February 2, 1924; Read February 19, 1924.]

(Plates I.-IV. \*; Text-figures 1-30.)

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INTRODUCTION.

Although much has been written about the anatomy of the Orang, no complete account of the structure of one animal exists. The fullest accounts hitherto published deal very fully with certain systems, but other parts were omitted because they were badly diseased or for some other reason. Many papers deal with the structure of small parts, but the organs which play very important parts in the animal economy, namely the joints, blood-vessels, lymphatics, ductless glands, and vagus and sympathetic nerves, have not received the attention which they deserve. Moreover, Sir Arthur Keith (42) points out that "there is not to be found anywhere in literature one complete account of the muscular system of the Orang." It is therefore evident that a detailed account of one animal is necessary to serve as a "type description" with which future work can be compared.

The animal on which the present account is based was a young female Bornean Orang which formed part of a collection of animals from Malaya presented to the Society by H.R.H. The Prince of Wales in May 1922. It died on July 7th, 1923, from a ruptured cerebral artery, possibly the result of a fall. All the viscera were healthy. Comparisons were made between it and several Gibbons, three Chimpanzees (♀ ♀ ♂), and parts of a

\* For explanation of the Plates, see p. 450.

Gorilla which Sir Arthur Koith kindly presented to me. The measurements of the body were as follows:—

	Inches
Length from inion to anus .. .. .	15·5
"    "    acromion to external humeral condyle.....	6·5
"    "    condyle to lower end of radius .....	7·25
"    of hand (carpus to root of middle digit 3·25, middle digit 3·75) .....	7·0
"    from great trochanter to centre of patella .....	5·0
"    "    centre of patella to lower end of tibia .....	5·25
"    of foot (sole 3·25; middle digit 4·0) .....	7·25
Excess of forearm over arm .....	0·75
"    "    upper extremity over lower extremity .....	2·80
Relation of hand to length of upper extremity .....	>25%

## THE MUSCULAR SYSTEM.

### *Muscles of the Head and Neck.*

The *platysma myoides* (text-fig. 1, PLA.) in this animal consists of a central and two lateral parts. The former arises from the fascia over the inner ends of the two pectoralis major muscles, and the latter arise from the fascia over the upper parts of the arms, the shoulders, and the mid-dorsal line of the neck. Between the central and lateral parts are triangular spaces containing fat. There is a marked decussation of fibres below the symphysis menti. Some fibres are attached to the lower border of the mandible, and others pass into the face to blend with the muscles of the lips and angle of the mouth. Some fibres end over the masseter. No splincter colli is present. Ruge (62) figures an origin extending from the mid-ventral line across the pectoralis major, deltoid, and trapezius to the mid-dorsal line. The origin is also extensive in the Gibbons, but it is more restricted in the Chimpanzee, Gorilla, and Man. The conditions in the Orang are as in many lower Mammalia. There is, however, no other trace of the panniculus carnosus.

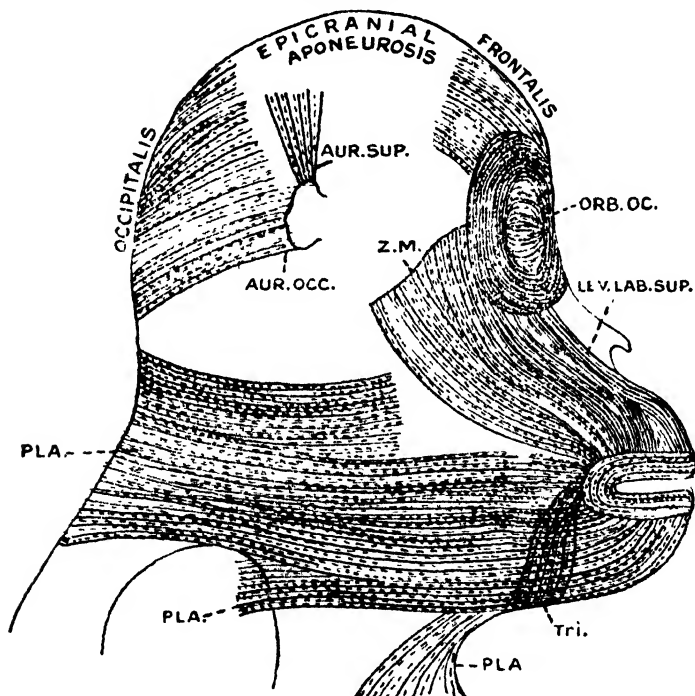
The *triangularis* (text-fig. 1, Tri.) is well defined, but small. The *risorius* is not differentiated as a separate muscle.

The *orbicularis oculi* (text-fig. 1, ORB.OC.) is relatively larger than in the Chimpanzee, for the orbital part covers wider areas of the bones bounding the orbital aperture; and the fibres are more closely packed than in the Chimpanzee. The whole muscle is considerably bulged forwards by the prominent eyeballs. The attachments of the orbital and palpebral parts are as in the Chimpanzee and Man, but these parts cannot be separated from one another. There is no marked ciliary bundle, and no slip runs to join the zygomatic mass. In two Chimpanzees such a slip was found, but it was absent in a third animal. Ruge (62) figures a small orbitalis. The narrow, cord-like internal tarsal

ligament is buried among the muscle fibres. The palpebral part is pierced by fibres of the levator palpebrae superioris.

The *zygomatic mass* (text-fig. 1, Z.M.) is not split up into distinct component parts, though the fibres are not very close together. Its linear origin runs downwards and backwards across the malar bone and anterior half of the zygoma. It is inserted into the orbicularis oris and skin of the upper lip close to the angle of the mouth. In this animal it is stronger than in Ruge's specimen, but it is weaker than in three Chimpanzees examined

Text-figure 1.



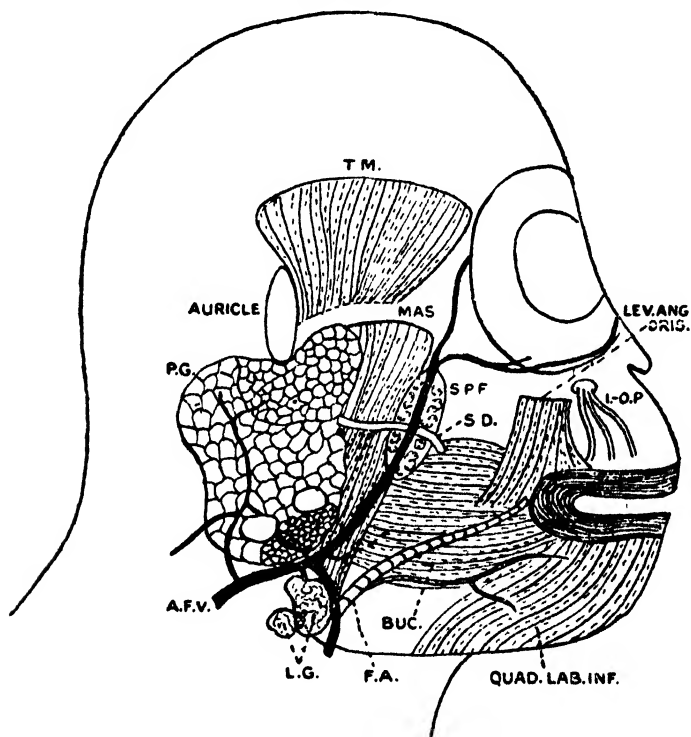
The superficial muscles of the head and neck. Letters in text.

by myself. Perhaps it presents many individual variations in the Orang as in the Chimpanzee. In one Chimpanzee I saw that the origin was linear.

The *levator labii superioris* (text-fig. 1, LEV.LAB.SUP.) lies partly under cover of the last muscle, from which it can be distinguished by its closely-set, reddish fibres. The origin, insertion, and relations are as in the Chimpanzee, and the innermost fibres form a levator alae nasi. Ruge (62) figured identical conditions.

The *levator anguli oris* (text-fig. 2, LEV.ANG.ORIS) in my specimen, as in Ruge's, is very powerful. It arises as in the Chimpanzee and Man. It blends with the orbicularis oris in the upper lip and at the angle of the mouth, and some fibres are inserted into the fascia over the buccinator. The Orang has thus a poor zygomatic mass and a large levator anguli oris, but the reverse is the case in the Chimpanzee.

Text-figure 2.



The deep muscles of the face and the structures related to them. A.F.V., anterior facial vein; F.A., facial artery; I.O.P., infraorbital nerve plexus; L.G., lymph glands; P.G., parotid gland; S.D., Stensen's duct. Other letters in text.

The *orbicularis oris* is as in the Chimpanzee and Man.

The *depressor labii inferioris* (text-fig. 2, QUAD.LAB.INF.) arises from the lower part of the outer surface of the mandible. It courses as in the Chimpanzee, but it does not touch the masseter behind.

The *buccinator* (text-fig. 2, BUC.) is covered anteriorly by the

caninus and posteriorly by an immense suctorial pad of fat (S.P.F.). It is relatively shorter than in the Chimpanzee, but its origin, insertion, and relations are as in the latter. The fibres do not decussate.

*Auricular Muscles* (text-fig. 1):—In this animal, as in Ruge's specimen, there is a superior auricular (AUR.SUP.) and an auriculo-occipital (AUR.OCC.). No tragus is present. Perhaps the examination of many specimens will show that they are variable as in the Chimpanzee.

*Nasal Muscles*:—I agree with Ruge that these consist of a levator alæ nasi running vertically and a nasalis running transversely. No depressor septi nasi is present.

The *masseter* (text-figs. 2 & 3, MAS.) is relatively more powerful than in the Chimpanzee and Man. It consists of the usual superficial and deep parts, but there is not a strong aponeurotic sheet between them. No sheet is present in the Gorilla and Gibbons, but it was well marked in three Chimpanzees, so it appears to be characteristic of that Ape. The superficial part of the masseter (S.P.M.) arises from the lower border of the malar bone and the anterior two-thirds of the zygoma; and the fibres, which are more curved than in the Chimpanzee, are inserted into the lower border and a small part of the angle of the mandibular ramus. The deep part of the masseter (D.P.M.), arising from the deep aspect of the malar bone and the entire length of the zygoma, is inserted into the upper two-thirds of the anterior half of the ramus of the mandible and the coronoid process. It has a rich blood supply, the arteries reaching it round the anterior and posterior borders of the ramus and through the sigmoid notch. The transverse facial vessels are smaller than in the Chimpanzee.

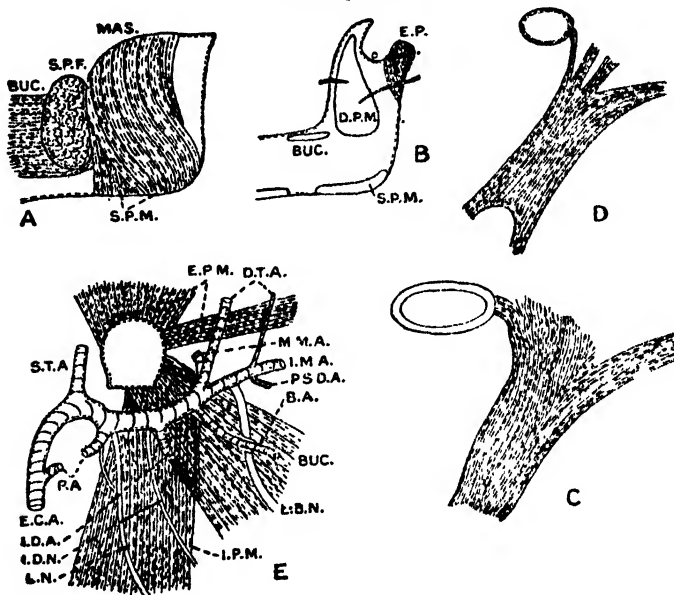
The *temporal muscle* (text-fig. 2, T.M.) in this very young animal arises from a convex line on the skull, whose upper limit is level with the upper border of the orbit. Posteriorly the origin reaches a little behind the auricle. It also arises from the temporal fossa and temporal fascia. At the origin the fibres are thin, but the muscle thickens as it passes behind the malar bone and anterior part of the zygoma to be inserted into the borders and apex of the recurved coronoid process as in the Chimpanzee. It receives its blood supply from the two deep temporal branches of the internal maxillary artery. One artery is nearly three times as large as the other, whereas they are equal in the Chimpanzee. Numerous authors have described how the muscles become larger and stronger as age advances, till they are separated on the vertex by a narrow interval or a sagittal crest.

*Pterygoid Muscles* (text-fig. 3 E) are in general as in the other Apes and Man. The short upper head of the external pterygoid (E.P.M.) is inserted almost entirely into the capsule of the temporo-maxillary joint, and the large lower head passes to the neck of the mandible. Both heads are separate, though in



contact at their insertions. The internal pterygoid (I.P.M.) is not peculiar. The general relations of the structures in the pterygoid region are as in the Chimpanzee, but in this very young animal the structures are closer together. The chorda tympani joins the lingual nerve (L.N.) well down in the region, and the internal maxillary artery (I.M.A.) has a long, horizontal part before it ascends over the lower head of the external pterygoid muscle.

Text-figure 3.



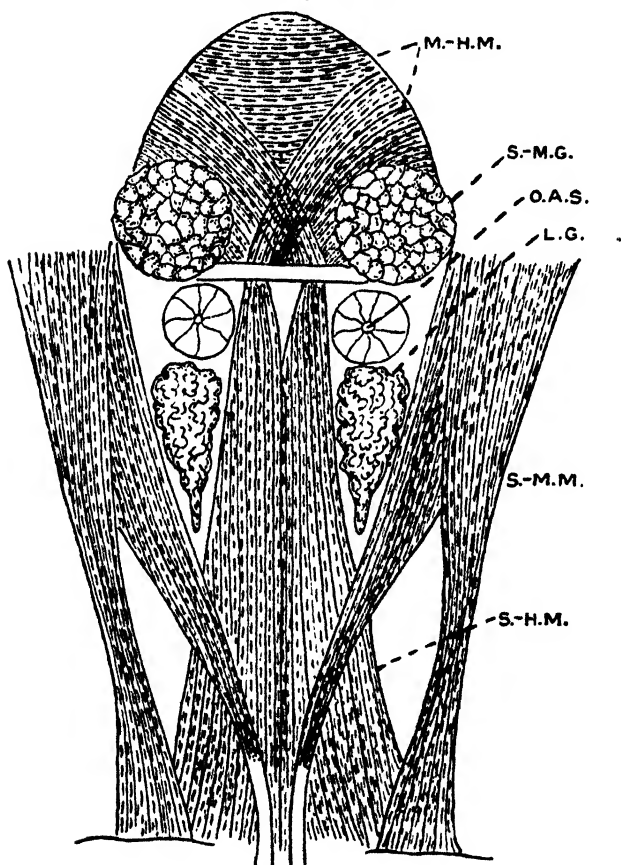
Muscles of the face. A. The masseter muscle and its relations: B. Attachments of muscles to the mandible: C, D. Variations in the zygomatic muscular mass in the Chimpanzee: E. The pterygoid region. B.A., buccal artery; BUC., buccinator; D.T.A., deep temporal arteries; E.C.A., external carotid artery; E.P., external pterygoid muscle; I.D.A., I.D.N., inferior dental artery and nerve; L.B.N., long buccal nerve; MAS., masseter muscle; M.M.A., mid meningeal artery; P.A., parotid arteries; P.S.D.A., posterior superior dental artery; S.P.F., suctorial pad of fat; S.T.A., superficial temporal artery. Other letters in text. Note the chorda tympani looping into the lingual nerve (L.N.).

The *levator* and *tensor palati* are horizontal as in the Chimpanzee. The *azygos uvulae* shows nothing peculiar except that it does not enter a uvula.

The *sterno-mastoid* (text-fig. 4, S-M.M.) consists of sternal and clavicular components, which remain separate, though closely apposed. The sternal head arises by a long, tapering tendon from

the front of the upper end of the manubrium sterni, and it is inserted into the mastoid ridge. The clavicular part arises from the inner third of the upper border of the clavicle; it gradually comes to overlap the sternal head, and it is inserted into the outer half of the occipital crest. This animal therefore possesses

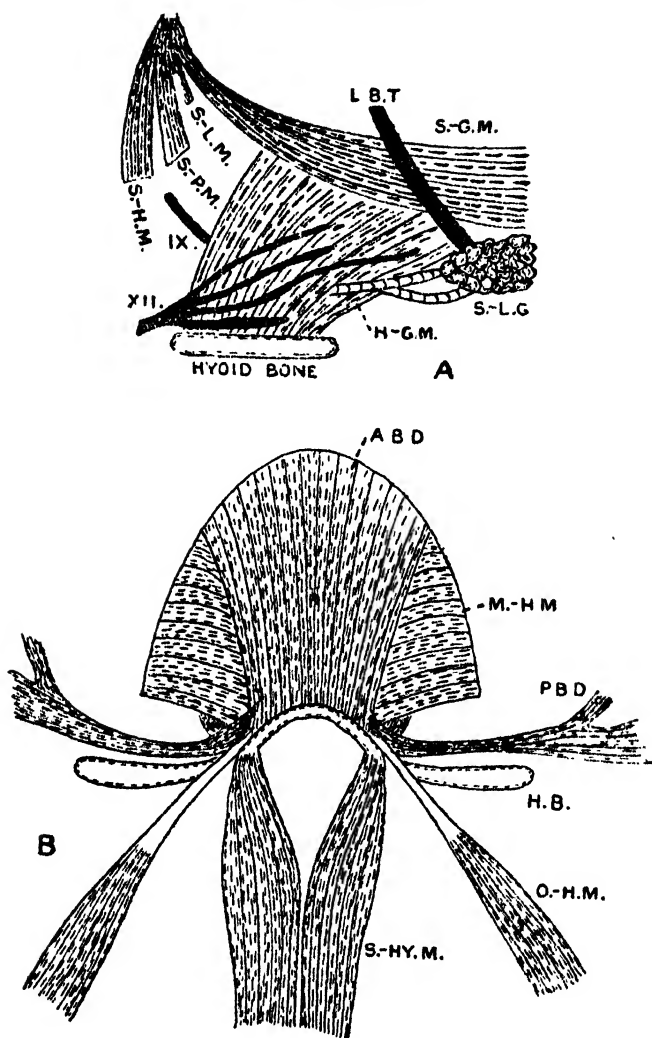
Text-figure 4.



The submental and cervical muscles. L.G., lymph glands; O.A.S., opening of air-sacs; S.-M.G., submaxillary gland. Other letters in text.

a sterno-mastoid and cleido-occipital. Fick (26) observed two parts fused below but separate elsewhere, Bischoff (7) described two parts separate throughout, and Vrolik (79) saw the clavicular head displaced to the acromion. The external jugular vein crosses the outer surface of the muscle. These conditions differ

Text-figure 5.



The submaxillary region in the Orang (A) and the hyoid muscles in a Chimpanzee (B). A.B.D., anterior belly of the digastric muscle; H.B., hyoid bone; L.B.T., lingual nerve; O-H.M., omo-hyoid muscle; M-H.M., mylo-hyoid muscle; P.B.D., posterior belly of the digastric; S-HY.M., sterno-hyoid muscle; S-L.G., sublingual gland; XII, hypoglossal nerve. Other letters in text.

from those in three Chimpanzees, for they had sterno-occipital and cleido-mastoids, and no external jugular vein lay on the surface of the sternal head. In one human fetus I observed separate sterno-occipital and cleido-mastoid parts of the muscle, and there was no fusion at any point.

The *sterno-hyoid muscles* (text-fig. 4, S-H.M.) run from the back of the sternum and inner ends of the clavicles to the lower border of the hyoid bone. They are wide below and narrow above. Fick (26) states that they are not easily separated in the middle line, but that is not the case in my specimen. In the angles between the lateral borders of the muscles and the hyoid bone lie the orifices through which the air-sacs communicate with the laryngeal ventricles. In the Chimpanzee, on the other hand, there is a single median communication.

The air-sac has thick walls, and the cervical muscles do not shine through them as they do in the Chimpanzee.

The *sterno-thyroid muscles* are as in the Chimpanzee.

The *omo-hyoid* is undivided and has no central tendon. It runs from the base of the scapula to the lower border of the hyoid bone at the side of the sterno-hyoid muscle. The tendon of insertion is long and slender. Fick (26) and Beddard (6) both mention it, and Bischoff (7) records absence of the muscles as an individual peculiarity. In the Gorilla, Gibbon, and most Chimpanzees the muscle has two bellies, but in one Chimpanzee it was as in the Orang (text-fig. 5). It is attached to the transverse scapular ligament in the Orang. In the Gorilla that ligament is absent.

The *digastric*, according to the observations of Adams (2), Bischoff (7), Fick (26), Owen (52), Sandifort (65), and myself, consists only of the posterior belly. It runs from the occipital bone to the angle of the mandible. It is thus a true depressor mandibulae. In all other Apes and in Man there are anterior and posterior bellies, but there is more or less fusion between the anterior bellies in the Apes.

The *mylo-hyoid* (text-fig. 4, M-H.M.) has similar attachments to the Chimpanzee, but the thin fibres decussate in a complicated manner. No submental lymph-glands lie on the surface of the muscle, in which condition the Orang agrees with the Chimpanzee and differs from Man. No raphé is present.

The *stylo-hyoid* (text-fig. 5, S-H.M.) runs from the styloid process to the body of the hyoid bone, and it is not tunnelled by the digastric as it is in many Mammals. Fick (26) stated that it is inserted into the air-sac, thus forming a stylo-laryngeus, but that muscle is separate in my specimen (S-L.M.). In one Chimpanzee the stylo-hyoid was not separate from the posterior belly of the digastric (text-fig. 5 B).

The *genio-hyoidei* and *genio-glossi* have the same attachments and relations as in the Chimpanzee, and the nerve supply is similar.

The *hyo-glossus* (text-fig. 5, H-G.M.) runs as in the Chimpanzee, but the anterior fibres are more horizontal. The relations are also as in the Chimpanzee, but the hypoglossal nerve has fewer branches on its surface; and no communication runs between the lingual and hypoglossal nerves along its anterior border. It is not fused with its neighbour, nor with the sterno-hyoid.

The *stylo-glossus* (text-fig. 5, S-G.M.) is as in the Chimpanzee. It arises along with the stylo-hyoid (S-H.M.), stylo-pharyngeus (S-P.M.), and stylo-laryngeus (S-L.M.).

The *stylo-pharyngeus* has the usual origin and insertion, but no fibres pass into the outer surfaces of the superior and middle constrictors as in some Chimpanzees.

The *constrictors of the pharynx* (text-fig. 6) have the usual arrangement, but the inferior constrictor (I.C.M.) is stronger than in the Chimpanzee; it arises from the whole length of the thyroid cartilage and from the cricoid; but no fibres arise from the tracheal rings. Fibres pass into it from the crico-thyroid (C-T.M.). It conceals the greater part of the middle constrictor (M.C.M.). The superior constrictor (S.C.M.) is as in Man.

The *thyro-hyoid* (text-figs. 6 & 21, T-H.M.) has a vertical origin from the upper half of the thyroid ala. The fibres converge, sweep round the tubular communication between the air-sac and larynx, and are inserted into the front of the hyoid bone. It is separated from its neighbour. It differs entirely from the muscle in the Chimpanzee.

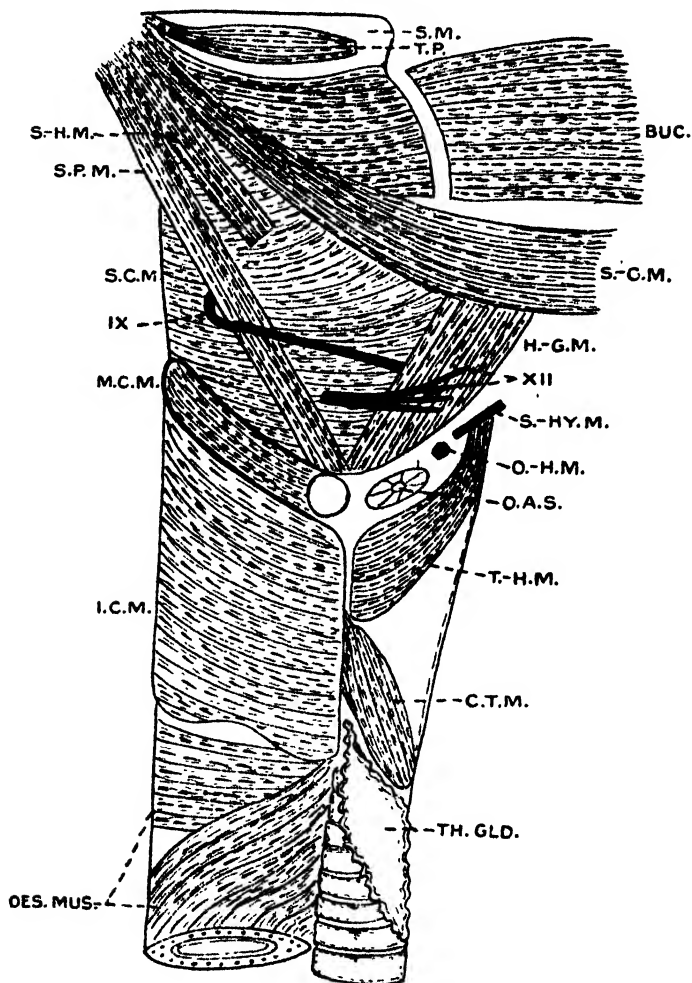
The *scalenus anticus* arises from the anterior aspect of the transverse processes of the third, fourth, and fifth cervical vertebræ, and is inserted into the scapula on the first rib. In one Chimpanzee (72) I found a similar origin, but in two others it arose from the fourth, fifth, and sixth transverse processes. It varies in different Gibbons, as it arises from a variable number of transverse processes between the third and sixth.

The *scalenus medius and posticus* are fused to form a single sheet, which runs from the posterior tubercles of the second to sixth cervical vertebræ. It is inserted into the inner inch of the upper border of the first rib—that is to say, its insertion runs from the inner end of the rib to beyond the angle. The size of the insertion is greater than that of the separate muscles in Man. The costal attachment is less than in the Chimpanzee (72).

*Prevertebral Muscles*:—The attachments are as follows. The longus colli and rectus capitis anticus major have a common origin from the seventh cervical and upper five thoracic centra. The bundle splits above into the vertical part of the longus colli and the rectus capitis anticus major. The former passes to a tubercle on the anterior arch of the atlas, and the latter runs to the basi-occiput. The upper oblique part of the longus colli is absent. The rectus capitis anticus minor runs from the lateral process of the atlas to the basi-occiput. The rectus capitis lateralis is absent.

It is evident that the arrangements of these muscles differ considerably from those in Man and the Chimpanzee (72). They

Text-figure 6.



Muscles of the pharynx. BUC., buccinator; OES.MUS., œsophageal muscles; O.A.S., opening of air-sac; S.M., sinus of Morgagni; S-H.M., stylo-hyoid muscle; T.P., tensor palati; TH.GLD., thyroid gland; IX., glossopharyngeal nerve curving round the stylo-pharyngeus muscle (S.P.M.). Other letters in text.

exhibit fusion which is frequently met with in muscles in other parts of the body.

*Muscles and Fasciæ of the Back.*

The outer surface of the trapezius is covered with strong fascia, which is weaker above than below; and its attachments are as in the Chimpanzee (72). No ligamentum nuchæ exists. It appears that the Gibbons are the only Apes possessing a ligamentum nuchæ.

The *trapezius* arises from the inner half of the occipital crest, the inion, the spines of cervical vertebræ 2-7, and the first seven dorsal spines and supraspinous ligaments. Hepburn (35) gives the occipital origin as extending out to the mastoid process. It touches the sterno-mastoid, thus forming an apex to the posterior triangle in this animal; in some specimens these muscles are not in contact. There is no tendinous origin in the middle spinal origin as there is in Man. The cervical part is short and thick as in the Gorilla and Chimpanzee, and it is assisted by the subjacent rhomboid sheet as pointed out by Sommer. In *Hylobates muelleri* I found the trapezius falling short of the occiput by four cervical vertebræ. It is inserted into the outer third of the clavicle, the acromion, and the whole length of the scapular spine, but there is no differentiation of fibres inserted into the base of the scapular spines as in Man and the Chimpanzee. There is no fusion with the deltoid.

The *latissimus dorsi* arises from the lower five dorsal spines and supraspinous ligaments, the posterior lamella of the lumbar fascia, and the outer lip of the crista ili between the two superior spines. The direction of the fibres is as in Man. It also gets slips from the outer surfaces of ribs 6-11, but Hepburn (35) states there is no costal origin. No slips are derived from the inferior angle of the scapula, and all Apes agree with one another and differ from Man in this respect. Its relations to the teres major and axilla are as in all Apes and Man, but the fibres fuse with the teres major close to the tendon of insertion. The strong, ribbon-like tendon has the usual insertion. The dorso-epitrochlearis is given off from the junction of the muscle and tendon. No dorso-humeralis exists.

The *rhomboideus* arises from the spinous processes of the cervical and upper six dorsal vertebræ, and a slip runs to the occipital crest (*rhomboideus capitis*). The muscle mass is not divided into major and minor muscles, and it is inserted into the entire length of the vertebral border of the scapula. Hepburn (35) gives its insertion as extending from the inferior angle to an inch above the base of the spine. It is longer at its insertion in the Orang and Chimpanzee than in the Gorilla and Man. Fick (23) mentions that there is no occipital origin. Bischoff (7) and others record an occipital origin, and Beddard (6) describes major, minor, and occipital rhomboids.

The *levator anguli scapulae*, in keeping with dimensions of the neck, is short. It arises from the transverse processes of cervical vertebræ 1-4. The slips of origin do not remain separate to

near their insertion as maintained by some observers. It is inserted into the costal aspect of the superior angle of the scapula. Various authors have given origins even as far down as the seventh cervical spine; and the muscle has been described as fusing with the serratus magnus as in many Marsupials. The levator scapulæ has been described as the serratus colli.

*Musculi Serrati Postici*:—The superior muscle is absent. The inferior muscle runs from the lumbar fascia to the outer surfaces and lower borders of the lower five ribs, as I observed in three Chimpanzees. Fick (26) mentions that the last slip only is well marked. The existence of this muscle is variable in the Gorilla. The superior and inferior muscles have been studied by Seydel (68), who found the superior muscle reduced to a few tendinous threads.

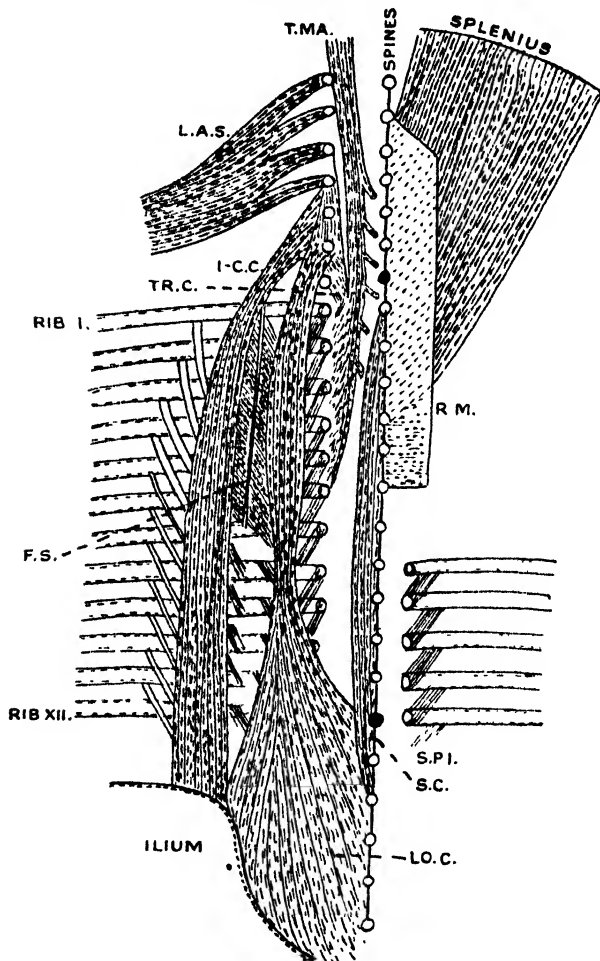
The *splenius* arises from the tips of all vertebræ, from the second cervical to the fourth dorsal, from the supraspinous ligaments, and from the strong fascia over the muscle itself. It is inserted, with the exception of the inner half inch, into the occipital crest down to the mastoid ridge. The splenius cervicis is absent in this animal, but Testut (74) saw one in his. The splenius capitis is, therefore, very strong. Possibly the examination of several animals would show variations in the splenius cervicis, for I observed variations in the Chimpanzee. The splenius cervicis had one to three digitations in three Chimpanzees. In Man the splenius cervicis varies, for it runs to three or four cervical transverse processes. I have already recorded the absence of the splenius cervicis in *Phascocomys* and the Phalangiers. In the sluggish arboreal Koala the splenius cervicis is present (71).

The *sacro-spinalis* (text-fig. 7) is strong, especially below. The ilio-costalis column is entirely separate from the longissimus, except at the origin. In three Chimpanzees I found them entirely separate in one animal and fused in the upper part of the thorax in two. The fusion has already been figured by me (72). It is possible that the examination of several Orangs would show individual variations. The muscle arises from the inner half of the iliac crest, the posterior sacro-iliac ligament, the back of the sacrum, the spines of the lumbar and upper sacral vertebræ, and the posterior lamella of the lumbo-dorsal fascia. The muscular mass separates into the usual columns, but the ilio-costalis and longissimus are more fused at their origins than in the Chimpanzee (72). The ilio-costalis, accessorius, and cervicalis ascendens are fused, and it is only below that any distinction between the first and second of these can be made out. Thus there is a long outer column or *ilio-costalis* (I-C.C.) which arises from the iliac crest, from all the ribs, and from a strong fascial septum (F.S.), which separates it from the longissimus. This septum reaches from the upper part of thorax down to the level of the seventh rib. Tendons are given off to the ribs, those to the first four being strong, whereas those to the lower



eight are slender. The column is also inserted by muscle fibres into the transverse processes of the fourth, fifth, and sixth cervical vertebrae behind the scaleni. At the insertion into the cervical transverse processes the ilio-costalis and longissimus are fused.

Text-figure 7.

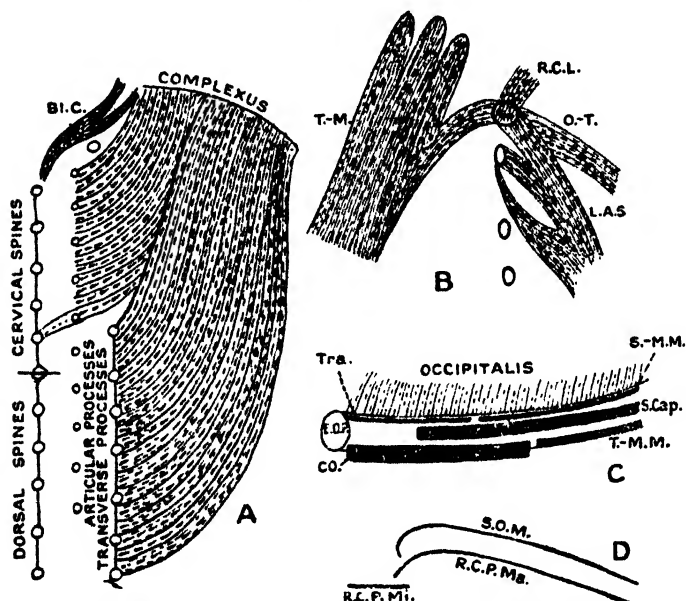


The sacro-spinalis muscle and its relations. L.A.S., levator anguli scapulæ; R.M., rhomboideus; S.P.I., serratus posticus inferior. Other letters in text.

The *longissimus* (LO.C.) is the most massive part of the sacro-spinalis, and it is more fleshy throughout than in Man. It is inserted externally into the thoracic transverse processes and

lumbar vertebræ. Some fibres are inserted into the septum, which separates it from the ilio-costalis. It is prolonged upwards into the neck as the *transversalis cervicis* (Tr.C.), which is inserted into the posterior tubercles of the second, third, fourth, fifth, and sixth cervical vertebræ internal to the ilio-costalis. It is fused with the *trachelo-mastoid* (T.Ma). The latter muscle arises from the lower four cervical articular processes and from the upper four thoracic transverse processes. It is also fused

Text-figure 8.



The deep muscles of the back in the Orang (A), and the insertions of the muscles on the occipital bone and atlas in the Chimpanzee (B and C). CO., complexus; E.O.P., inion; O.-T., omo-trachelian; L.A.S., levator anguli scapulæ; R.C.L., rectus capitis lateralis; R.C.P.Ma. and R.C.P.Mi., rectus capitis posterior major and minor; S.Cap., splenius capitis; S.-M.M., sternomastoid muscle; S.O.M., superior oblique; T-M. and T.-M.M., trachelo-mastoid; Tra., trapezius.

with the complexus. It is inserted in the occipital crest under the splenius capitis. The *spinalis dorsi* (S.C.) is as in the Chimpanzee. In the Chimpanzee (text-fig. 8 B) the trachelo-mastoid has a digitated insertion into the occiput and atlas.

The *complexus* (text-fig. 8 A) arises from the transverse processes of the first six dorsal vertebræ, the lower five cervical articular processes and the spine of the seventh cervical vertebra. It is inserted into the occipital bone below the superior curved

line; and the length of the insertion is a little more than half the distance between theinion and mastoid. On the inner side of the muscle, but in no way connected with it at the origin, is a Y-shaped bundle of fibres which are very slender. The vertical limb arises from the fascia on the inner side of the complexus, and the two diverging limbs blend with the insertion of that muscle. This is all that could be called a biventer cervicis (B.C.). The complexus is not divided into separate bundles as in three Chimpanzees examined by myself; in one of these animals I described and figured the muscle (72). None of the three Chimpanzees had any trace of a biventer cervicis. With the exception of the trapezius, the splenius capitis and complexus are the most powerful muscles in the neck in the Orang and Chimpanzee.

The *semispinalis* is more extensive than in Man and differs from that in the Chimpanzee (72). The *spinalis dorsi* arises from the transverse processes of the lower seven dorsal vertebræ, and it is inserted into the spinous processes of the last two cervical and first four dorsal vertebræ. The *semispinalis cervicis* arises from the transverse processes of the first four dorsal vertebræ and from the articular processes of the lower four cervical vertebræ; it is inserted into the spinous processes of cervical vertebræ 2-5.

The *multifidus spinæ* has the usual characters and attachments. These are similar in all essentials to those in Man and the Chimpanzee.

*Sub-occipital Muscles*:—The sub-occipital triangle is obliterated by the overlapping of the inferior oblique and rectus capitis posticus major by the superior oblique, and by the fact that the adjacent borders of the first two muscles are in contact. These muscles, likewise the rectus capitis posticus minor, have the same attachments as in Man. The superior oblique may be called immense, and the rectus capitis posticus minor is less covered by the major muscle than in the Chimpanzee. In three Chimpanzees I observed variations in the degree in which the triangle is obliterated; and in one animal (72) only did I observe an accessory triangle. The insertions of the posterior cervical muscles in the Chimpanzee are shown in text-fig. 8 C and D.

The *levator costarum* are of the same number as in Man, namely twelve pairs, and their attachments are similar to those in him and in the Chimpanzee (72).

The *rotatores dorsi*, *interspinales*, and *intertransversarii* are as in Man and the Chimpanzee.

When the characters of the back muscles in the Apes are examined as a whole, it is seen that individual variations occur in the following characters:—

1. Extent of the cervical origin of the rhomboidens.
2. Degree of fusion of the ilio-costalis and longissimus.
3. Extent and character of the insertions of the ilio-costalis and longissimus.

4. The tendons of the ilio-costalis to the ribs are powerful above and weak below, or *vice versa*.
5. The fusion of the longissimus and splenius cervicis.
6. The size of the splenius cervicis.
7. The degree of fusion of the ilio-costalis and scaleni.
8. The degree of obliteration of the sub-occipital triangle.
9. The prominence of the rectus capitis posticus minor.
10. The extent of the origin of the levator anguli scapulæ.
11. The presence or absence of the posterior serrate muscles.

#### *Muscles of the Arm.*

The *pectoralis major* (text-fig. 9) is divided into three parts—clavicular, costo-sternal, and abdominal—and a diverticulum of the air-sac separates the first and second. The clavicular part, which maintains a uniform thickness, arises from the extreme inner end of the clavicle and the front of the manubrium sterni (Hepburn (35) gives no clavicular origin). The cephalic vein dips behind it. The second part arises from the front of the lower half of the sternum and from the cartilage of the last true rib. The third part arises from the fascia over the external oblique muscle of the abdomen. The second and third parts unite to form a common muscle which joins the outer end of the clavicular part; and the combined muscle is inserted into the pectoral crest from the great tuberosity of the humerus downwards. No differentiation of a pect. quartus occurs. The total length of the aponeurotic insertion is a third of that of the humeral shaft. The nerves reach the muscle by turning round the *pectoralis minor*.

The delto-pectoral triangle contains fat, lymph-glands, and the cephalic vein; so it differs from that of the Chimpanzee. Its fat is drained by a vein to the external jugular vein.

The separation between the clavicular and costo-sternal parts is a point of difference between the Orang and Chimpanzee; and in one Chimpanzee I observed total obliteration of the delto-pectoral triangle.

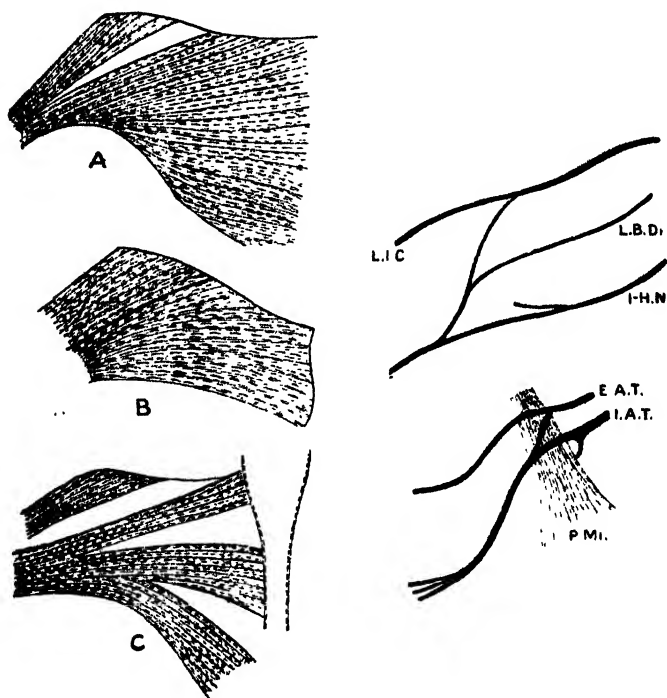
Various authors have described different arrangements. Fick (26) records three parts entirely separated. Bischoff (7) and Sandifort (65) describe absence of the clavicular head; and Beddard (6) mentions two parts which unite before their insertion.

The *pectoralis minor* is separated from the *pectoralis major* by a prolongation of the air-sac. It has a continuous origin from the second, third, fourth, and fifth costal cartilages (Hepburn, 3 and 4 ribs), and it is inserted into the upper part of the coracoid process of the scapula from behind the apex to the bend. Fick (26) states that it is inserted into the upper surface of the process, and Bischoff (7) gives its insertion as the root. It differs, therefore, from that in the Chimpanzee and Man. Beddard (6) describes the muscle as consisting of two parts, which

are inserted into the coracoid and humerus. Duckworth (20) figured a double muscle in the Gorilla, and I myself observed a double muscle in a Chimpanzee. So it is evident that it can be single or double in each of the higher Simiidae. The nerves to the pectoral muscles are shown in text-fig. 9 C.

The *subclavius* is as in the Chimpanzee. The costo-coracoid membrane is poor, but the costo-coracoid ligament is strong and the tendon of the pectoralis minor plays over it. Hepburn (35) described an additional origin from the second rib.

Text-figure 9.



The great pectoral muscles in Man (A), the Chimpanzee (B), and the Orang (C). The figures on the right are the external and internal thoracic (E.A.T. and I.A.T.), intercosto-humeral (I-H.N.), lesser internal cutaneous (L.I.C.) and lateral branch of the first dorsal (L.B.Di.) nerves; P.Mi., pectoralis minor.

The *deltoid* arises from the front of the outer half of the clavicle, the outer border of the acromion, the lower border of the spine of the scapula, and the fascia over the infra-spinatus; but the latter is more extensive in the Chimpanzees. The fibres converge to the usual deltoid insertion, and there is no fusion with the pectoralis major. The muscle is not divided into parts.

*Scapular Muscles*:—The *infraspinatus* is larger than the *supraspinatus*, but both are much as in the Chimpanzee. The *teres minor* arises from a little more than the lateral half of the axillary border of the scapula, and its mesial extremity is strongly fused with the *infraspinatus*; it is a very powerful muscle. The insertions of the *supraspinatus*, *infraspinatus*, and *teres minor* are restricted to the great tuberosity of the humerus. The *subscapularis* arises from the whole of the subscapular fossa, and is inserted by muscular and aponeurotic fibres into the lesser tuberosity of the humerus. It is fused with the *teres major*, and Fick (26) also observed fusion. The lateral border close to the humerus and up to its insertion is followed by the anterior humeral circumflex artery. It is relatively more powerful than in the adult Chimpanzee. It is not divided into sections as in the Gorilla, which has seven parts. The *teres major* arises from the mesial third of the axillary border of the scapula; and it has the usual humeral insertion. Its origin is fused with the *subscapularis*, and its insertion is fused with the *latissimus dorsi*. The accounts of Beddard (6) and Fick (26) regarding the scapular muscles are very similar to the above. Hepburn (35) shows that the origin of the *teres major* is less in the Gorilla and Orang than in other Apes.

The *biceps* arises as in the Chimpanzee. The two bellies likewise unite at the junction of the lower and middle thirds of the arm. The muscle does not develop its ribbon-like tendon till it passes the level of the humeral epicondyles. The tendon is chiefly developed in connection with the long part of the muscle, the part derived from the short head being implanted into the tendon. The tendon, which is long and powerful, has the usual radial insertion. There is no *lacertus fibrosus* as many authors have recorded.

The *coraco-brachialis* arises from the coracoid process along with the short head of the *biceps*. In its middle part it has an interval through which the musculo-cutaneous nerve passes. It is inserted into an inch of the middle third of the inner surface of the shaft of the humerus some distance from the deltoid insertion. The lowest fibres fuse with the *brachialis anticus*. No fibres run to the dorso-epitrochlearis and internal intermuscular septum, and there is no *coraco-brachialis brevis*. The musculo-cutaneous nerve passes through the interval between the two parts of the muscle. Church (14) and Hepburn (35) describe similar conditions.

The *brachialis anticus* consists of two parts, which only come together in the distal half. The inner part arises from the median half of the front of the humerus up to a point about a sixth of an inch above the lowest point of the deltoid insertion; and it is fused with the *coraco-brachialis*. The outer part arises from the lateral half of the front of the humerus and extends well above the insertion of the deltoid. The two parts are separated by a fissure in the upper part of their course.

Distally they unite to form a very powerful muscle, which is inserted into the inner side of the coronoid process.

The *dorso-epitrochlearis* is similar to that in the Chimpanzee. The ulnar nerve pierces the internal intermuscular septum between it and the triceps.

*Triceps*:—The long head arises from the lower part of the outer surface of the lip of the glenoid fossæ and from the lateral half of the axillary border of the scapula. It joins the outer head of the muscle, whose line of origin extends from the insertion of the teres minor above to the level of the musculo-spiral nerve below where it winds round the humerus; and the long head is fused proximally with the brachialis anticus. The combined long and outer heads receive the inner head, whose origin is from the whole length of the humerus distal to the insertion of the teres major. It is, therefore, evident that the extent of origin of the long head is the only essential difference between the muscle in the Orang and Man. The insertion is as in Man. It is continued into the anconeus.

The origin of the flexor muscles from the internal condyle of the humerus is very well marked.

The *palmaris longus* is well developed, and its characters are as in Man. Hepburn (35) and Beddard (6) describe a similar arrangement, but Fick (26) recorded a very complex muscle. In his specimen the tendon divided into three strips, which joined the abductor pollicis brevis, the palmar fascia, and the flexor brevis minimi digiti. Vrolik (79) and Hepburn (35) observed it in all Apes. I observed it in two Chimpanzees out of three animals examined; Bischoff stated that it is absent in the Gorilla; and Keith (42), who made an exhaustive study of this muscle in the African Simiidae, found it present in four out of eleven Gorillas, and in nine out of twelve Chimpanzees. It is not always present in Man.

The *flexor carpi radialis* arises under cover of the palmaris longus from the internal condyle of the humerus. It is fused with the flexor sublimis digitorum and pronator radii teres. It receives fibres from the radius down to a point at the junction of the fourth and last fifth of the shaft of the radius. Fick (26) and Langer (46) described origins as far down as the lower fourth of the radius. The tendon is inserted into the palmar aspect of the bases of the second and third metacarpals. Beddard (6) mentions the second metacarpal only, but Hepburn (35) records the insertion as the second and third metacarpals. The radial origin is as extensive in two out of three Chimpanzees examined, but it was greater in a third animal (73). On the lateral side of the muscle lie the radial and superficial volar artery.

The *pronator radii teres* arises as in the Chimpanzee (72). It is inserted into the second fifth of the outer surface of the shaft of the radius. The median nerve passes between its coronoid and condylar heads. Hepburn (35) points out that

the muscle has no coronoid head in the Gorilla and Gibbon. Langer (46) and Fick (26) both describe long insertions in the Orang, and give actual figures comparing it with Man.

The *flexor carpi ulnaris* has a muscular origin from the flexor condyle, and an aponeurotic origin from the olecranon. It is attached by fascia to the olecranon, and it receives fibres from the flexor sublimis digitorum. It has the usual insertion into the pisiform. The ulnar nerve enters the forearm between its two heads.

The *flexor sublimis digitorum*, or flexor perforatus, arises by coronoid, condylar, and radial parts as in the Chimpanzee, and there is continuity between it and the flexores carpi radialis and ulnaris. The condylar head passes to the fourth and fifth digits. The coronoid head is also attached to the condylar head; it joins the radial head to form a muscle whose tendons go to the second and third digits. This arrangement is somewhat like that in the Gibbon. It differs from that in the Chimpanzee (72) and Gorilla, but Hepburn (35) states that it is similar to that in them. The radial head also fuses with the condylar head. The tendon sheaths are more powerful than in Man. There is nothing peculiar in the splitting and insertion of the tendons.

The *flexor profundus digitorum* consists of radial and ulnar segments, which are quite separate except at the upper part. The ulnar segment arises from the upper two-thirds of the front and outer aspects of the shaft of the ulna, and from the interosseous membrane; it also derives fibres from the flexor carpi ulnaris and deep fascia uniting the muscle to the ulna; it provides the deep flexor tendons to the medius, annularis, and minimus. The radial segment arises from the same extent of the radius and from the interosseous membrane; it provides the deep flexor tendon to the index. The tendon to the pollex is not attached to the tendon of the radial segment, so the arrangement differs from that in the Chimpanzee and Gibbon, and resembles that in some Gorillas (35). The pollical tendon, however, is not provided with a muscular belly like the flexor longus pollicis in Man. Hepburn (35) has given a detailed account of the evolution of the flexor muscles. The fusion of the deep flexors and flexor sublimis is a trace of the past history of the muscles. Fick (26) and Gegenbaur describe how there is no flexor longus pollicis connected to the profundus. Vrolik (79), on the contrary, described one.

**Thenar Muscles:**—In their general arrangement these muscles resemble those of the Chimpanzee. The abductor pollicis brevis is not divided into slips as in some Chimpanzees (72); it arises entirely from the anterior annular ligament. The opponens pollicis has the same attachments as in the Gorilla, Chimpanzee, and Man; it is very strong. The flexor brevis pollicis has outer and inner heads as in the Gibbon and Chimpanzee; and the outer head is not divided into slips as I observed in the Chimpanzee. The adductores are described later.



*Hypothenar Muscles*.—These are generally disposed as in the Chimpanzee (72). The abductor minimi digiti has a long muscular belly and a short tendon, whereas the reverse was the case in three Chimpanzees described by myself. In all other respects the muscles were identical.

*Lumbricales*.—The four lumbricales are long and slender, and they begin to arise from the deep flexor tendons in the lower part of the forearm. They remain close to the flexor tendons throughout. The first arose from the radial side of the index flexor, the second from the radial side of the flexor of the medius, the third from the adjacent sides of the flexors of the medius and annularis, and the fourth from the radial side of the flexor of the minimus. Hence the origin differs from that in Man and the Chimpanzee. The first and second muscles are not connected by a slip; but I observed this connection in three Chimpanzees.

*Adductores Pollicis*.—These are the only representatives in the Orang of the contrahentes group described by Bischoff (7), Cunningham (15), Halford (33), and Hepburn (35). The adjacent margins of the transverse and oblique muscles were in contact in this animal, but the muscles can easily be distinguished. The adductor transversus is fasciculated, but the fibres of the adductor obliquus are close together. In the Gibbons the adductor muscle is not separable into two parts. The adductor transversus arises from a septum running along the palmar aspect of the third metacarpal, and the adductor obliquus arises from the base of the third metacarpal and the tendon of the flexor carpi ulnaris. The origin differs from that in Man and all the Apes except the Gibbons (35). The muscles are inserted together into the ulnar side of the base of the proximal phalanx of the thumb.

*Interossei*.—There are three palmar and four dorsal interossei as in Man and all the Apes except the Chimpanzee (72), which has three additional palmar interossei derived from the dorsal series.

The *pronator quadratus* is well marked and connects the distal quarters of the radius and ulna. It is not weak, nor are the fibres very oblique as Hepburn (35) points out. Fick (26) also describes a small muscle.

The *supinator longus* arises from the upper two-thirds of the external supracondylar ridge, but the origin does not extend as high up as the insertion of the deltoid. It is not fused with the brachialis anticus. It appears to consist of two parts—upper and lower—which soon fuse. Its insertion into the lower inch of the shaft of the radius is longer than in the Chimpanzee (72).

The *extensor carpi radialis longior* arises from the lower part of the external supracondylar ridge and septum and from the external humeral condyle. Its tendon is inserted into the dorsal aspect of the base of the metacarpal bone of the index finger. It is crossed by tendons of the extensors of the thumb.

The *extensor carpi radialis brevis* arises from the external condyle of the humerus, the external intermuscular septum, and the external lateral ligament of the elbow joint. It is closely applied to, but not actually fused with, the last muscle. Its tendon is inserted into the dorsal aspect of the base of the third metacarpal bone. It is very like the corresponding muscle in the Chimpanzee in its origin from the ligament of the elbow-joint.

The *extensor communis digitorum* consists of two parts. One of these parts arises from the common extensor origin and from the septa between it and the muscles on its sides. It gives off three tendons to the minimus, annularis, and medius. The other arises from the lower parts of the internal surfaces of the radius and ulna, the overlying fascia, and the interosseous membrane; it supplies tendons to the index and medius. Hepburn (35) states that the muscle is as in Man, but that is not so in this animal. It differs, too, from the condition which I have already recorded in the Chimpanzee (72). Fick (26) and Beddard (6) also describe conditions similar to those in Man. The tendons are inserted in the same manner as in Man, and the tendons which run to the medius from the two parts of the muscle unite to form a common dorsal expansion.

The *extensor indicis* shows nothing peculiar in its origin and insertion. Its tendon is very long and slender, and is closely applied to the lateral part of the extensor communis.

The *extensor minimi digiti* arises from the common extensor origin, the intermuscular septa between it and adjacent muscles, and from the lower part of the extensor communis. It gives tendons to the annularis and minimus.

The *extensor carpi ulnaris* has the usual origin and the usual insertion into the base of the fifth metacarpal bone. Its tendon is one of the strongest on the dorsum of the hand.

It is therefore evident that two extensor tendons act on each of the four fingers:—

*Index*: extensor indicis and lower part of extensor communis.

*Medius*: both parts of extensor communis.

*Annularis*: upper part of extensor communis and extensor minimi digiti.

*Minimus*: as in annularis.

*Extensors of the Thumb*:—The three extensors arise as in the Chimpanzee, but the insertions differ somewhat. The extensor *ossis metacarpi pollicis* runs to a sesamoid bone and the base of the first metacarpal. The extensor *primi internodii pollicis* runs to the base of the first metacarpal. The extensor *secundi internodii pollicis*, which is inserted into the base of the ungual phalanx, gives an expansion to the first phalanx.

The *supinator brevis* is thicker above than below. It has the usual characters, and its insertion reaches distally as far as the middle of the shaft of the radius.

*Serratus Magnus*:—This muscle consists in this animal of two

distinct parts, and the upper part of the proximal portion is greatly thickened. The proximal part arises by three digitations from the upper three ribs, the first one being very thick; it is inserted into the vertebral border of the scapula in its upper three-fourths. No slip arises from the fourth rib, so there is a gap between the two parts of the muscle. The distal part arises by six digitations from ribs 5-10 inclusive; it is inserted into the lower fourth of the vertebral border of the scapula. The first part is innervated by the fourth, fifth, and sixth cervical nerves and is supplied by the vertebral artery. The second part is supplied by the seventh cervical nerve and long thoracic artery.

*Muscles of the Thorax, Abdomen, and Pelvis.*

The *intercostal muscles* do not differ in any essential point from those in Man. No *sternalis* is present.

*External Oblique*:—This muscle arises from the lower borders and outer surfaces of ribs 6-12. They interdigitate with the digitations of origin of the serratus magnus, but there are no digitations with the latissimus dorsi. The posterior fibres have no direct attachment to the pelvis. They all pass to the aponeurosis, which is attached to Poupart's ligament and the middle line, where it is fused with the opposite aponeurosis. Poupart's ligament is a very feeble structure, and is not connected to the other abdominal muscles. Mesial to the external oblique, and separated from it by a narrow gap, is a thin stratum of fibres running between the iliac crest between the superior spines and the lower border of the last rib.

*Internal Oblique*:—The internal oblique arises from the iliac crest between the superior spines and from the deep fascia in the outer two-thirds of the space between the anterior superior iliac spine and the pubis. The fibres run as in Man. They are attached to the lower borders of the last four ribs, and into the aponeurosis, which has the usual attachments. The muscle fibres of the lower part of the muscle almost reach the linea semilunaris. The aponeurosis of the external oblique joins the aponeurosis of the internal oblique in the linea semilunaris.

*Transversalis Abdominis*:—The fibres arise from the deep surfaces of the lower six ribs by slips which interdigitate with the diaphragm, from the lumbar fascia, and from the anterior half of the inner lip of the iliac crest. The lower fibres are widely separate, but the upper fibres form a thick muscle. The aponeurosis, which receives a film of tissue from the aponeurosis of the internal oblique, forms the posterior wall of the sheath of the rectus abdominis.

The sheath of the rectus is not complete, and its formation differs from that in Man and the Chimpanzee. In the anterior part the aponeurosis of the internal and external oblique muscles unite in the linea semilunaris, and a thin membrane, arising from the cord-like linea, forms the anterior wall of the sheath. The

posterior wall of the sheath is formed by the transversalis aponeurosis. The internal oblique aponeurosis does not split. In the posterior part the sheath is better marked, for the transversalis aponeurosis is connected to the aponeurosis of the internal oblique.

The *rectus abdominis* has five tendinous intersections in this animal. It has a single origin from the upper end of the symphysis pubis, and it is inserted into the ensiform cartilage and fifth, sixth, and seventh costal cartilages. The *pyramidalis* is absent as in three Chimpanzees examined by myself. Fick (26) points out that it is absent.

The *diaphragm* arises from the back of the sternum and from the lower six ribs by digitations. When the origin is viewed from the abdomen a continuous muscular origin is seen, and no arcuate ligaments are visible. Fibres rise from the last rib, the fascia over the quadratus lumborum and psoas, and the vertebral column, the latter arising by crura which are wide and muscular. The origin differs from that in Man and the Chimpanzee in the close connection between the diaphragm and the muscles of the posterior abdominal wall. The central tendon is relatively larger than in the Chimpanzee. The diaphragm is pierced by openings as in Man; and the chief point of difference is that the vena azygos major does not go through the aortic opening along with the aorta and thoracic duct; the œsophageal branch of the celiac axis is replaced by a branch of the coronary artery. The arteries supplying it are branches of the celiac axis (see page 407). It is innervated as usual by the phrenic and sympathetic nerves.

The *psoas parvus* arises by strong tendons from the sides of the bodies of the last dorsal and first lumbar vertebra. The thin belly ends in a long powerful tendon, which is inserted into the posterior part of the ileo-pectineal line. At its lower part the tendon is connected to the fascia over the psoas major. The tendon widens close to its insertion, which is farther back than in the Chimpanzee, in which respect it agrees with the Gorilla. Hepburn (35) describes conditions as above.

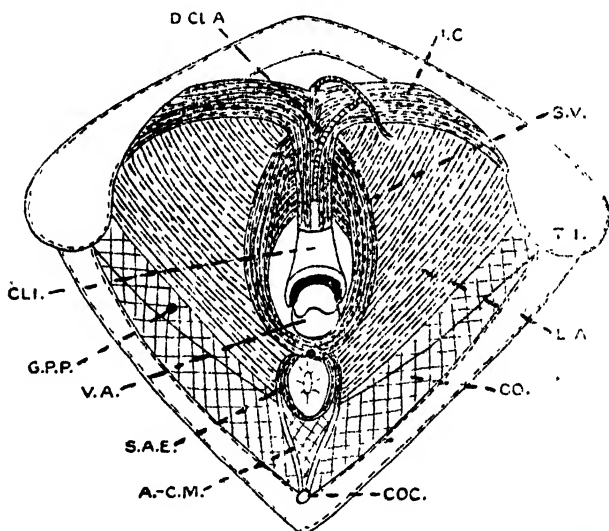
The *psoas magnus*, according to Hepburn (35), arises from the last dorsal and all lumbar vertebrae. In this animal it arises from the sides of the bodies of all lumbar vertebrae and the last dorsal vertebra, from the intervertebral discs between these vertebrae, from the lumbar transverse processes, and from the surface of the quadratus lumborum. It unites with the iliacus to form the ilio-psoas, which is inserted into the lesser trochanter of the femur.

The *quadratus lumborum* arises from the inner part of the iliac crest, the ilio-lumbar ligament, and the lower lumbar transverse processes. Its fibres are continuous with those of the iliacus as in the Chimpanzee. It is inserted into the lower border of the last rib and the upper transverse lumbar processes.

The *iliacus* shows nothing peculiar.

*Muscles of the Perineum* (text-fig. 10):—The *ischio-cavernosus* (I.C.) muscles are powerful. They arise from the inner surfaces of the pubic rami by broad bases, and they meet on the dorsum of the clitoris, along which they pass to a point half-an-inch proximal to the free extremity. A branch of the pudendal artery emerges from the pelvis over it and gives off the dorsal artery of the clitoris (D.Cl.A.). The *sphincter vaginae* (S.V.) runs from the central point of the perineum behind to the root of the clitoris in front. Some fibres blend with the ischio-cavernosus on the dorsum of the clitoris. Fibres of the sphincter ani externus (S.A.E.) blend with it in the central point of the perineum. No vestibular bulbs lie beneath it. The *transverse perineal muscles* are absent as in the Chimpanzee (72).

Text-figure 10.



The pelvic and perineal muscles. CL.I., clitoris; COC., coccyx; G.P.P., gap in pelvic musculature; T.I., tuber ischii; V.A., vagina. Other letters in text.

The *sphincter ani externus* (text-fig. 10, S.A.E.) forms a thick collar round the anus. It is attached anteriorly to the central point of the perineum. Postero-laterally it is connected to the ano-coccygeal membrane.

The *ano-coccygeal membrane* (A-C.M.) divides into two parts which run to the sides of the gut, where they are blended with the levator ani and sphincter ani externus.

Fibres of the levator ani pass to the skin, where they form the *corrugator cutis ani*.

The pelvic floor is chiefly composed of the coccygeus. The *levator ani* (text-fig. 10, L.A.) arises from the pelvic brim over

the anterior half of the ilium. It is inserted into the front and sides of the anus. Between it and the coccygeus is a narrow gap. The fascia over the coccygeus is attached to the levator ani. The *coccygeus* (text-fig. 10, CO.), arises from the side of all vertebrae from the third sacral to the tip of the coccyx. It is inserted into the tuber ischii and posterior border of the ischium up to the level of the top of the acetabulum.

### *Muscles of the Leg.*

The *gluteus maximus* is thin and divided into upper and lower parts. The former springs from the sacrum and great sacro-sciatic ligament. The latter arises from the ischial tuberosity, and is closely fused with the short head of the biceps. The interval between the parts in this specimen is not as great as would appear from Hepburn's account. The insertion into the shaft of the femur is strong, and stops short of the external condyle by a little less than three-quarters of an inch. Hepburn describes it as stopping at the level of the middle of the external intermuscular septum. Fick (26) states that there is no sacro-tuberosus (great sacro-sciatic) ligament. In all other Apes and in Man the muscle is not split into segments.

The *tensor fasciæ femoris* is absent, whereas it is present in a feeble condition in the Chimpanzee and Gorilla.

The *gluteus medius* is very similar in its origin and insertion to that in the Chimpanzee (72), but its tendon of insertion is not split by the vastus externus. It is closely associated with the tendon of the pyriformis at its insertion into the great trochanter. In the Chimpanzee a slip connects the *gluteus medius* and *pyriformis*.

The *gluteus minimus* is weak. It runs from the posterior part of the dorsum ilii to the anterior border of the great trochanter, where it is associated with the *scansorius*, which is stronger than in the Gorilla and Gibbon, but about the same size as in the Chimpanzee (72). The *scansorius* helps flexion of the hip joint, and is useful in climbing, like the dorso-epitrochlearis in the upper extremity, with which it has been homologized. Fick (26) points out that it possesses the same function as the *gluteus minimus*, with increased power of internal rotation. The part played by the muscle has received considerable attention from that author (see (26) page 37).

The *obturator internus* is a strong muscle, arising as usual within the pelvis. It is inserted into the trochanteric pit of the femur above and in front of the tendon of the *obturator externus*. Its long, strong tendon receives a strong inferior gemellus and a weak superior gemellus. Fick (26) and Hepburn (35) describe the gemelli as similar to the above.

*Biceps Flexor Cruris*:—The two heads remain separate. The long head, which arises from the ischial tuberosity along with the *semitendinosus* and *gluteus maximus*, is inserted into the outer

side of the tuberosity of the tibia, and a fibrous expansion connects it to the external femoral condyle. Church (14) describes it as being inserted into the lower third of the femur, and Hepburn (35) describes an insertion into the capsule of the knee joint. Fick (26) reviews the literature dealing with the long head. He points out that Vrolik, Duvernoy, and Huxley regarded it as a piece of the gluteus maximus, whereas Bischoff, Henke, and Langer showed its true character. The short head arises from the third quarter of the shaft of the femur on its posterior aspect; it is inserted into the head of the fibula and the fascia over the gastrocnemius, but it has no connection with the long head. Fick (26) gives a very long origin from the femur, and Hepburn (35) mentions union with the long head at its insertion. In two Chimpanzees out of three I observed strong fusion between the bellies of the long and short parts of the biceps.

The *semitendinosus* arises along with the long head of the biceps, and it is fused for about three-quarters of an inch with the semimembranosus. It has an extensive aponeurotic insertion into the deep fascia in the upper third of the inner side of the leg.

The *semimembranosus* is inserted into the postero-mesial aspect of the internal tuberosity of the tibia. It has no expansions to the fascia of the leg.

The *rectus femoris*, contrary to the arrangements described by several authors, has only one head of origin, but a fibrous septum runs through the muscle. There is a long aponeurotic origin from the anterior border of the ilium in the region of the anterior inferior spine and from the bone around the upper border of the acetabulum. It is inserted into the upper border of the patella. The *vastus internus* is fused with the crureus. It springs from the lower two-thirds of the linea aspera and from the septum between itself and the adductor magnus. The lower half becomes tendinous, and is inserted into the inner border of the patella and capsule of the knee joint. The *vastus externus* arises from the outer border of the linea aspera and from the upper third of the septum between itself and the biceps muscle. It is inserted into the outer border of the patella. There is a certain amount of fusion between it and the crureus. It does not split the tendon of the gluteus medius as in the Chimpanzee. No *subcrureus* was found. Fick (26) states that the quadriceps is as in Man, and Hepburn (35) points out that it is not so easily separable into its component parts as in him.

The *sartorius* is relatively weaker than in the Chimpanzee. It arises by a narrow aponeurosis from the ilium below the anterior superior spine, and it is inserted into the upper three-quarters of an inch of the inner border of the tibia. Between it and the gracilis there lie the saphena vessels and nerve, but no bursa. Fick (26) describes a more extensive origin from the ilium, and its insertion lower down between the upper and middle thirds of the tibia. Langer (46) states that it is inserted into the deep

fascia of the leg. And Beddard (6) describes a slender muscle with a broad tendinous insertion into the tibia above the *gracilis* and *semitendinosus*. In my specimen it receives a large nerve close to its insertion.

The *gracilis* is not adherent to the *sartorius* as it is in the Chimpanzee. It arises by an aponeurosis from the front of the symphysis and upper part of the ascending ramus of the pubis. The fibres end in a narrow tendon, which afterwards expands to be inserted into the deep fascia and into the three-quarters of an inch of the inner border of the tibia immediately distal to the insertion of the *sartorius*.

The *adductor longus* has a short origin from the pelvic brim on the horizontal ramus of the pubis. It is inserted into the linea aspera on the third quarter of the femoral shaft. It is not at all fused with the more ventral *adductor magnus*. Fick (26) points out that it arises in the adult from an ilio-pectineal tubercle. It is partly fused with the *vastus internus* at its insertion.

The *adductor brevis* is under cover of the *adductor longus* and *adductor magnus* at its origin from the front of the horizontal ramus of the pubis. It is inserted into the femur between the *pectineus* and *gluteus maximus*. It is coarsely fasciculated, but not divided into bellies as in the Chimpanzee.

The *adductor magnus* has a very extensive origin from the front of the entire length of the symphysis pubis, the descending ramus of the pubis, and the ischial tuberosity. The extent of the origin, which is quite continuous, is similar to that in the other Apes. It divides into two parts, whereas it is divided into three in the Chimpanzee. The upper part, which is comparatively thin but strong, is inserted into the middle two-fourths of the back of the shaft of the femur. The lower part of the muscle is inserted into the back of the shaft of the femur immediately behind the first part; it gives off a strong fasciculus, which is inserted into the inner condyle of the femur and the bone a short distance above it. The two parts of the *adductor magnus* are fused in their middle parts, and the insertion of the upper parts of the muscle is in contact with the insertion of the *adductor longus*. Beddard (6) describes a muscle consisting of two parts, and Hepburn (35) points out that the Orang is the Ape in which the muscle most resembles that in Man. The condylar fasciculus is crossed by the *saphena* vessels and nerve, and separates them from the superficial femoral vessels dipping down to become the popliteal vessels.

The *pectineus* runs from the horizontal ramus of the pubis to the shaft of femur below and behind the lesser trochanter and insertion of the *ilio-psoas*. It is closely opposed to the inner border of the *adductor longus*.

The *quadratus femoris* arises from the outer part of the ischial tuberosity. Close to its insertion it splits into two parts, which are attached respectively to the femur behind the lesser trochanter and above the *pectineus* and to the *pectineus* and to the back of the great trochanter.



The *obturator externus* is much as in Man. It is, however, closely related to the tendon of the *obturator internus* at its insertion into the digital fossa on the inner surface of the great trochanter of the femur.

The *tibialis anticus* arises from the upper two-thirds of the anterior and lateral aspects of the tibia. The upper quarter of this origin blends with the *extensor longus digitorum* superficial to the *extensor longus hallucis*. A short distance from its origin it splits into two bellies, each of which has a stout tendon developed within it, like the shaft within a feather. Thus the splitting is greater than in the Chimpanzee (72). One tendon is inserted into the medial aspect of the proximal end of the shaft of the first metatarsal bone; and the other tendon runs to the plantar aspect of the internal cuneiform and joint-capsule.

The *extensor longus digitorum* arises in its upper quarter along with the *tibialis anticus*. It also arises from the upper two-thirds of the inner surface of the shaft of the fibula. It is inserted by four long tendons into the outer four toes. The insertions are triple in each case. Lateral bands go to the base of the first phalanx. And a central band, which blends with the fascia over the first phalanx, also runs to the second phalanx and first interphalangeal joint. Bands connect the tendons.

The *extensor longus hallucis* runs from the upper three-quarters of the inner surface of the shaft of the fibula to the base of the terminal phalanx of the hallux. No strong fibrous pulley was seen as in the Chimpanzee.

The *peroneus tertius* is absent.

The *extensor brevis digitorum* arises from the os calcis by four bellies which are separated by septa. The first one runs almost transversely to the base of the dorsum of the first phalanx of the hallux. The others are inserted into the dorsal expansion of the tendons of the *extensor longus digitorum* of the index, middle, and fourth toes.

The *peroneus brevis* arises from the middle two-fourths of the front and outer surface of the shaft of the fibula, and is inserted into the base of the fifth metatarsal bone. It is fused in the upper part of its origin with the *peroneus longus* and *extensor longus digitorum*. I did not observe the tendon divided into separate slips as Hepburn (35) mentions on the left side, but it divided into three on the right side, and these were inserted into the tubercle and base of the fifth metatarsal bone and to the expansion of the *extensor tendon* to the fifth digit.

The *peroneus longus* arises from the upper half of the front and outer surfaces of the fibula. It is fused with the *peroneus brevis* and *extensor longus digitorum* in front, and with the flexor muscles behind. The tendon has the usual course, and is inserted into the base of the first metatarsal bone. Its course across the sole is horizontal.

The *gastrocnemius* has the usual two heads of origin. The

inner head rises from the back of the internal epicondyle of the femur and posterior ligament of the knee joint. The outer head arises from the postero-lateral aspect of the external femoral epicondyle; it is thinner and wider than the inner head. There is in this specimen very little fusion between the muscular bellies, for the fibres are inserted into the sides of a long aponeurosis, which becomes the tendo Achillis lower down. The two bellies are of equal length, whereas the inner one is the longer in the Gorilla and Chimpanzee. The fibres reach down very close to the os calcis.

The *soleus* has no tibial origin. It arises from the posterior aspect of the head of the fibula by an aponeurosis which blends with the outer head of the gastrocnemius. Some fibres are fused with the subjacent flexor muscle sheet. It is inserted into the deep aspect of the tendo Achillis almost to the os calcis.

The tendo Achillis is inserted obliquely in the os calcis, and a bursa intervenes between it and the bone. The method of fixation pulls up the heel and inner side of the foot and depresses the outer part.

The *popliteus* arises by a thin, strong tendon from the lateral epicondyle of the femur. It is triangular in shape, and composed of coarse bundles which are inserted into the popliteal line of the tibia and the bone above it. The muscle is about an inch long. There is no trace of a division into two parts as in the Chimpanzee (72). The nerve-supply is as in Man.

The *flexor muscles* consist of fibular and tibial parts, but a few fibres run between them. They do not form a continuous stratum, but Hepburn (35) states that they do.

The *flexor longus hallucis*, which is better described as the flexor digitorum fibularis of Pagenstecher and v. Bardeleben, arises from the femur and fibula by two heads. One head arises from the external condyle of the femur and the external lateral ligament of the knee joint. The other springs from the head and upper half of the shaft of the fibula, and fibres blend with the peroneal muscles. The fibres end in a powerful tendon, which breaks up into slips which are inserted into the third and fourth digits. Hepburn (35) and Fick (26) give the insertion as the third and fourth digits, no tendon going at all to the hallux. They give a more limited origin to the muscle than I have described above.

The *flexor longus digitorum*, or flexor digitorum tibialis, arises from the upper two-thirds of the inner surface of the shaft of the tibia, and its tendons are inserted into the second, fourth, and fifth toes, the tendon to the fifth toe being slender. Hepburn (35) and Fick (26) give the insertion as the second and fifth digits.

From my own observations and from the records of other writers I have come to the conclusion that there is individual variation in the disposition of the tendons of the flexor fibularis, flexor tibialis, and flexor brevis digitorum.

The *tibialis posticus* arises under cover of the flexor muscles described above, and the origin is much as in Man and the other Anthropoid Apes. It is inserted into the under surface of the scaphoid bone and sheath of the tendon of the peroneus longus. The scaphoid insertion is spread out over the bone.

The *abductor hallucis* has a strong belly and a cord-like tendon. It arises from the inner aspect of the os calcis, and its outermost fibres are blended with the innermost fibres of the flexor brevis digitorum. It is not in contact with the abductor minimi digiti as Hepburn (35) points out. The tendon is inserted into the base of the first phalanx of the hallux. Hepburn describes the muscle as receiving fibres from the internal annular ligament and inner side of the foot as far as the scaphoid; and these fibres go to the inner side of the proximal part of the first metatarsal bone. In my specimen these fibres are absent.

The *flexor brevis digitorum* arises from the front and inner aspect of the os calcis, and it is partly overlapped by and fused with the abductor hallucis. It gives two slender tendons to the second and third digits. Hepburn (35) mentions three tendons to the second, third, and fourth toes, the latter being a mere adjunct to the flexor longus digitorum. The origin of the muscle shows a tendency to division into superficial and deep bellies.

The *abductor minimi digiti* has a long origin from the greater part of the length of the os calcis and the sheath of the tendon of the peroneus longus. Its long tendon is inserted into the base of the proximal phalanx of the fifth digit. No other insertions were detected in this animal, though Hepburn (35) describes other attachments.

The *flexor brevis hallucis*, as Hepburn (35) fully describes, consists of a large inner and a small outer head, the former being similar to that described in my paper on the Chimpanzee (72), only the insertion is longer.

The *flexor brevis minimi digiti* runs from the plantar aspect of the fifth metatarsal bone and sheath of the peroneus longus. It does not receive a slip from the base of the fourth metatarsal bone as described by Hepburn (35). It is inserted into the outer side of the base of the proximal phalanx of the fifth toe.

The *opponens minimi digiti* is not present as a separate muscle. Fick (26) and Hepburn (35) pointed out that it is absent. The *accessorius* is also absent.

The *adductor hallucis* arises from a raphe extending along the plantar aspect of the third metatarsal bone from the tarsus to the metatarsophalangeal joints; and the posterior limit of the muscular origin is the tendon of the peroneus longus. The insertion and division of the muscle into transverse and oblique parts are as in the Chimpanzee (72). No other contrahentes are present.

*Interossei*:—Four dorsal and three plantar muscles exist, and the basal line as regards their action runs through the third digit. The only point of special note is the inner head of the first

dorsal interosseous muscle, which arises, according to Hepburn (35), from the internal cuneiform bone. In my specimen the arrangements are similar to those described by Hepburn.

*Lumbricales*:—The first, third, and fourth muscles arise from the tibial aspects of the long flexor tendons, and the second springs from the adjacent sides of the first and second long flexor tendons. The insertions are not peculiar. Other authors describe similar arrangements.

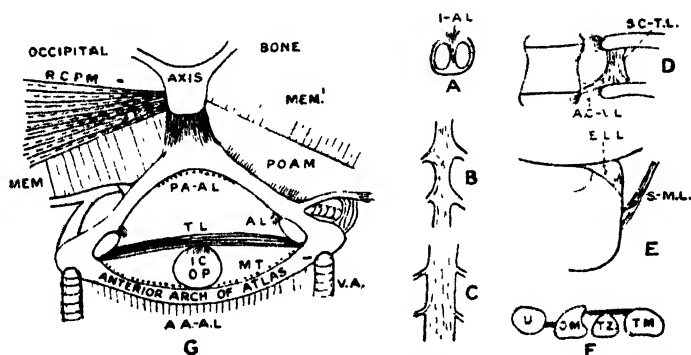
### THE JOINTS.

*Temporo-mandibular Joint* (text-fig. 11 E):—The glenoid cavity is shallower than in Man. It is bounded behind by a large post-glenoid process, but there is no marked eminentia articularis in front. The large post-glenoid process prevents the mandible from having such a close relation to the external auditory meatus as in Man. The joint has a delicate capsule. The *external lateral ligament* (E.L.L.) forms a triangle with the base attached to the zygoma. It is not divided into anterior and posterior parts as in Man. The fibres sweep downwards and backwards, and some run down along the posterior border of the ascending ramus of the mandible. The *stylo-mandibular ligament* (S-M.L.) is represented by several strands attached higher up than in Man. On removing the capsule and external ligament the *articular disc* appears. This is a very thin lamina of cartilage attached to the capsule. It is not perforated. The upper surface is almost flat, and the lower surface is concave. It fits closely on to the condyle of the mandible. No fibres of the external pterygoid muscle pass into it. The capsule is thinner internally than on the front, back, and outer sides. The *spheno-mandibular ligament* is delicate. Fick (26) states that the joint is as in Man.

*Costo-vertebral Joints* (text-fig. 11 A & B):—In this young animal the capsules are lax. The *anterior costo-vertebral ligament* (A.C-V.L.) differs from that in Man and the Chimpanzee (72). It has only the inferior part strongly developed, the rest of the ligament being composed of short, weak fibres. Within the capsule an *interarticular ligament* (I-A.L.), running from the head of the rib to the lateral surface of the intervertebral disc, divides the cavity of the joint into upper and lower parts. When the rib is removed, it is seen how the inter-articular ligament passes to the head of the rib between two oval articular cartilages (A). The costo-transverse articulation has a synovial membrane and capsule. The *superior costo-transverse ligament* (text-fig. 11 D. S.C-T.L.) is a strong radiating band running from the neck of the rib to the lower border of the transverse process above. It blends with the anterior costo-vertebral ligament of its own head and with the capsule of the costo-transverse joint above. The *middle and posterior costo-transverse ligaments* are not easily defined, particularly the latter. No superior costo-transverse ligament runs from the first rib.

*Inter-vertebral Joints*:—The *anterior common ligament* has the same extent and characters as in Man. It is particularly strong and mixed with dense connective-tissue fibres in the lumbar region. It receives fibres from the costo-central ligaments. The *supraspinous ligament* is weak in the dorsal region, and it is sometimes impossible to detect it, for the spinal muscles are so closely related to the spinous processes. It is well marked in the lumbar region. No *ligamentum nuchæ* exists. The *interspinous ligaments* are short and the *intertransverse ligaments* are delicate. The *posterior common ligament* (text-fig. 11 B & C) runs as in Man. It is, however, wider over the centre than in him, and the processes over the deep surfaces of the intervertebral discs are narrower. The *ligamenta subflava* have the usual elasticity, and the capsules of the interneural joints are as in Man.

Text-figure 11



The spinal, costal, temporo-mandibular, and carpal ligaments. O.M., os magnum; T.M., trapezium; T.Z., trapezoid; U., unciform bone. Other letters in text.

*Atlanto-axoid Joint*:—The *anterior atlanto-axoid ligament* (text-fig. 11 G, A.A-A.L.) runs from the front of the axis to the anterior arch of the atlas. It is powerful and pointed. Its base runs below into the anterior common ligament. Above it is connected to the anterior atlanto-occipital ligament. The *posterior atlanto-axoid ligament* (P.A-A.L.) corresponds to the *ligamenta subflava* elsewhere. It does not possess a series of strengthening or accessory bands as in the Chimpanzee (72). The capsular ligament of each atlanto-axial joint is strengthened by an *accessory band* (A.L) running from the deep surface of the lateral mass of the atlas to the upper edge of the body of the axis.

*Occipito-atlantal Joint* (text-fig. 11 G):—The *anterior occipito-atlantal ligament* is a thin membrane running from the anterior arch of the atlas to the anterior margin of the foramen magnum. Laterally it is continuous with the capsules of the joint between

the occipital condyles and atlas. It has a strengthening band on each side of the middle line, but there is a single median band in Man. The *posterior occipito-atlantal ligament* (P.O.-A.M.) is also a membrane. It is continuous laterally with the capsular ligaments. Below it is fixed to the upper border of the posterior arch of the atlas, and above it is attached to the posterior border of the foramen magnum. It is very short from above downwards, and it is not to be mistaken for a sheet of fascia running from the arch up to the deep surface of the rectus capitis posticus major and the occipital bone under cover of it. This sheet receives strong additions from the anterior border of the spine of the axis vertebra (text-fig. 11 G, MEM.). Strong fibres run from the spine of the axis to the atlas and membrane.

On the posterior arch of the atlas on its upper border there is a small tubercle pointing laterally. To it is attached a strong ligament which is connected to the lateral mass of the atlas, the posterior occipito-atlantal membrane, the capsule of the crinio-vertebral joint, and the occipital bone. It completes a small ring through which the vertebral artery (V.A.) can be seen (text-fig. 11 G).

The *cruciate ligament* has no superior crus, but the transverse (T.L.) and inferior parts (I.C.), particularly the former, are strong. The *middle odontoid and check ligaments* are short, for the odontoid process protrudes for a small distance into the posterior cranial fossa.

The inferior articular surfaces of the atlas are as in Man, whereas those in the Chimpanzee differ, being reniform like the superior articular surfaces (text-fig. 12 A).

*Scapular Ligaments*:--The transverse scapular ligament is beginning to ossify in this young animal. The spino-glenoid ligament is absent.

*Acromio-clavicular Joint*:--The acromio-clavicular ligament is composed of strong fibres, particularly those at the bottom. Fibres of the deltoid and trapezius are attached to the ligament. No inter-articular fibro-cartilage exists. The whole joint is relatively stronger than in Man.

The *coraco-acromial ligament* arises from the greater part of the lateral side of the coracoid process; and it splits into two parts. One part is inserted into the under surface of the clavicle in its outer ninth, overlapping the trapezoid ligament. The other part is attached to the upper surface of the acromion, and strengthens the acromio-clavicular ligament. No sub-acromial bursa was seen.

*Coraco-clavicular Ligament*:--The trapezoid part arises from the upper and lateral aspect of the coracoid process; its insertion is split. The conoid ligament is as in Man, and there is a bursa between it and the trapezoid ligament. Fick (26) states that it is difficult to separate the component parts from one another.

The *coraco-humeral ligament* is weak. It runs to the fovea and the sheath of the subscapularis.

Speaking generally, the ligaments of the shoulder girdle are stronger than in Man. The coracoid process is mobile in this animal, and articulates by a globular expansion with the scapula. Fibres of the shoulder capsule help to form ligaments of a coraco-scapular joint.

*Shoulder Joint*:—The capsule is attached to the humerus and scapula as in Man. The superior *gleno-humeral ligament* is well defined, but the middle and inferior ligaments were not detected with certainty. The *labrum glenoidale* is represented by a slight thickening round the entire scapular articular cartilage. No *transverse humeral ligament* exists. The *long head of the biceps* is attached to the cartilaginous articular surface of the scapula, no tubercle being as yet present. It is also connected to the synovial sheath.

*Elbow Joint*:—The *capsule* receives, and is strengthened by, fibres of the triceps behind and the brachialis anticus in front. Many fine arterial branches are seen ramifying on the back of the capsule; these lie among fat which lies between the triceps and capsule. The capsule is attached above the coronoid fossa, and crosses the humerus almost horizontally from condyle to condyle; it is attached below to the margins of the coronoid process and orbicular ligament. Posteriorly the attachments are as in Man. The fibres run in all directions. The *external lateral ligament* is as in Man, but it is relatively weaker. The *internal lateral ligament* consists of a strong anterior part and a weak posterior part. No transverse ligament exists. The *orbicular ligament* is of great strength. The *oblique cord* is as in Man.

Fick (26) points out that the axis of the joint is such that the forearm comes to lie on the chest in flexion. Extension is not complete as in Man.

The *inferior radio-ulnar joint* has a strong palmar and a weak dorsal ligament connecting the radius and ulna.

*Radio-carpal Joint*:—The *lateral ligaments* are as in Man, but the internal one is strongly reinforced by a prolongation of the sheath of the flexor carpi ulnaris over the pisiform bone. The *posterior ligament* is as in Man. The *anterior ligament* contains oblique fibres running downwards and inwards from the radius, and straight fibres descending from the ulna. The *recessus saciformis* is exceedingly well marked and large, as is the *discus articularis*.

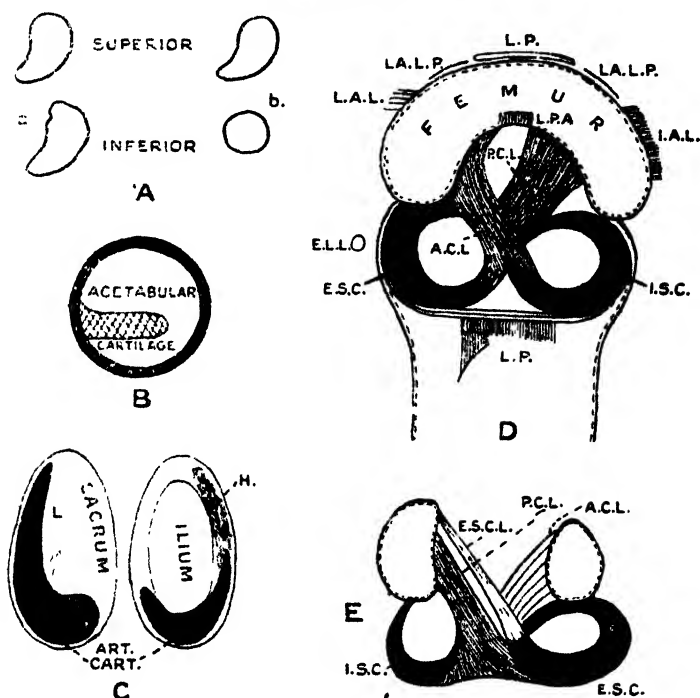
*Carpal Joints*:—The dorsal ligaments radiate from a centre at the os magnum as in Man, whereas they do not do so in the Chimpanzee (72). The palmar ligaments are as in Man. The pisiform bone gives attachment to strong *piso-metacarpal* and weak *piso-hamate* ligaments. The *interosseous ligaments* of the proximal carpal bones are as in Man. In the distal row of carpal bones, interosseous ligaments connect the four elements together. The ligament from the unciform to the os magnum is deep; but the ligament from the os magnum to the trapezium is more superficial, and is united to the head of the trapezoid bone

(text-fig. 11 F). The interosseous ligament runs from the trapezium to the scaphoid. The *synovial cavity* forms one sac only. The *collateral ligaments* are as in Man, but the external one is very strong.

*Carpo-metacarpal Joints*:—These have palmar, dorsal, and interosseous ligaments. The first joint is as in Man. The bases of the metacarpal bones are connected together by dorsal and palmar transverse metacarpal ligaments.

*Metacarpo phalangeal Joints*:—These are as in Man.

Text-figure 12.



The joints. A, articular processes of the atlas in the Chimpanzee (a) and Orang (b). B, acetabulum: C, sacro-iliac joint opened (L., ligaments; H., articular surface; ART.CART., articular cartilage): D, knee joint of the Orang opened from the front (L.P.A., interarticular ligament): E, knee joint of the Orang opened from behind. Other letters in text.

*Inter-phalangeal Joints*:—The capsules are themselves weak, but the prominent ones are strengthened by connections with the sheaths of the tendons passing over them. The internal and external ligaments are as in Man.

*Lumbo-sacral Joint*:—The ligaments are as in Man, except that no lateral lumbo-sacral ligament exists. The joint between the



centre is not so prominent as in Man, owing to the thinness of the intervertebral disc.

Cunningham (16) has shown that the amount of consolidated lumbar curvature is inversely proportional to the degree of extensibility of the hip joint. Thus the Chimpanzee has a good lumbar curve, and the hip can be extended till it forms an angle of  $131^{\circ}$ , open forwards, with the long axis of the back. In the Gibbon the curve is less and the angle is  $146^{\circ}$ . In the Orang there is practically no curve, and the hip can be extended to form an angle of  $153^{\circ}$ , open backwards, with the long axis of the back.

The *symphysis pubis* has the usual ligaments, but the posterior and superior ligaments are poor.

*Lumbo-iliac and Sacro-iliac Joints*:—In this very young animal there is considerable mobility of the iliac bones on the sacrum. The *ilio-lumbar ligament* is a strong band running from the tip of the fourth lumbar transverse process to the inner border of the iliac crest. The fibres of the *inferior ilio-lumbar ligament* are poorly defined. The *anterior sacro-iliac ligament* is of great strength. It courses as in Man and the Chimpanzee (72). The bands running along the pelvic brim are very noticeable. The *short posterior sacro-iliac ligaments* are very poorly defined indeed. The *oblique posterior sacro-iliac ligament* differs from that in Man and the Chimpanzee. It is a strong cord running from the posterior inferior iliac spine to the side of the coccyx, and it is bound to the sacrum on the way. In Man its upper attachment is the posterior superior spine. The *great sacro-sciatic ligament* is present. Fick (26) states that it is absent. The *small sacro-sciatic ligament* is absent. On cutting into the capsule of the sacro-iliac joint (text-fig. 12 C) the sacrum is seen to have a strongly convex, crook-shaped articular surface, whereas the ilium is hollow and incompletely covered by cartilage. The hollow of the crook lies posteriorly, and inter-articular and capsular fibres are attached to the bone within it.

*Hip Joint* (text-fig. 12 C):—The head of the femur is small and globular. The joint has a considerable range of movement, and the relation of the extensibility to the lumbar curvature has been described above. The *capsule* is lax, but its attachments are much as in Man. The *ilio-femoral ligament* is not a distinct Y-shaped band as it is in Man. It is represented by small fibres radiating from the region of the anterior inferior iliac spine to the capsule and anterior intertrochanteric line. It could not check the body from rolling backwards if the body were erect as it does in Man. The *pudo-capsular ligament* consists merely of thickened fibres of the capsule. The capsule is strongest posteriorly and inferiorly. The *cotylloid ligament* is very thick, and the *transverse acetabular ligament* is long and wide marked. The *ligamentum teres* is absent, and most authors describe it as such. The *acetabular articular surface* differs from that in Man. In Man there is a ribbon-like band of cartilage extending from the brim of the cavity, but it does not cover the

floor of the cup; it is widest on its supero-posterior aspect, and narrowest at the anterior margin of the notch. In the Orang the upper half of the cavity is covered with a hemisphere of cartilage and the lower quarter by a small arc. Between them is a broad strip of floor devoid of cartilage. The cotyloid ligament is attached all round the outer margin of the articular cartilage. *Retinacula* are absent. But there is a thin fatty layer constituting the so-called *Haversian gland*. No synovial bursæ exist.

*Knee Joint* (text-fig. 12 D & E):—In this dead animal with the muscles intact I was unable to fully extend the knee joint. The *ligamentum patellæ* (L.P.) is strong. It has the usual attachments. On each side of it there is a *lateral patellar ligament* (La.L.P.), which is an expansion of the tendon of one of the vasti muscles. The internal lateral patellar ligament is weaker than the outer one. The *posterior ligament* is best studied by putting tension on the tendon of the semimembranosus. The ligamentum posticum Winslowii passes from the deep surface of the tendon across the back of the knee capsule, and some fibres pass to the popliteal surface of the femur above the internal condyle. From the horizontal central band fibres pass upwards and downwards to the popliteal surface of the femur above the intercondylar notch, the external condyle of the femur, and the posterior border of the tibia. The popliteus muscle arises from it so it has no tunnel for the muscle as in Man. The *lateral ligaments of the knee* have the same attachments as in Man, but the internal one is not so definitely divided into anterior and posterior portions.

When the joint is opened, it is seen that a stout inter-articular ligament connects the deep surface of the ligamentum patellæ (L.P.) to the intercondylar area on the front of the femur. The *anterior cruciate ligament* (A.C.L.) is narrow, thin, and strong. Above, it is attached to the external condyle and the femur between the condyles. Below, its fibres are attached to the tibial spine, the mesial parts of the two articular surfaces, and the two anterior cornua of the semilunar cartilages. The *posterior cruciate ligament* (P.C.L.) is thicker than the anterior cruciate ligament. It arises from the upper surface of the tibia behind the spine, and it is inserted into the lower part of the non-articular outer surface of the internal condyle of the femur. Behind it lies the tense cord-like ligament (E.S.C.L.) connecting the posterior horn of the external semilunar cartilage to the internal condyle above the posterior cruciate ligament. The posterior cruciate ligament is connected by fibres to the posterior cornua of both semilunar cartilages. The *transverse ligament*, which is not strong, connects the two semilunar cartilages (T.L.). The *internal semilunar cartilage* (I.S.C.) is semicircular. Its anterior cornu is attached closely to the non-articular area on the tibia in front of the anterior cruciate ligament, but it receives some fibres from the ligament. The posterior cornu is attached to the non-articular surface on the head of the tibia in front of the attachment of the

posterior cruciate ligament. Fibres pass into it from the posterior ligament. The capsule and internal lateral ligament are attached to its side. The *external semilunar cartilage* (E.S.C.) is semicircular. Its anterior cornu is attached closely to the non-articular surface of the head of the tibia in front of the spine, and it receives a strong band from the anterior cruciate ligament. The posterior cornu receives fibres from the posterior cruciate ligament, and is connected by a strong, cord-like ligament to the external condyle of the femur. It is thus evident that the cartilages have shorter cornual connecting bands than in Man.

The external cartilage is semicircular in Man and the Orang, but the cartilage and its cornual ligamentous bands form an almost complete circle in Man. In the Chimpanzee and Gorilla the external cartilage forms a complete cartilaginous circle.

No infrapatellar pad of fat and ligamentum mucosum exist, but the *lateral alar ligament* (L.A.L.) is powerful. The *internal alar ligament* (I.A.L.) is weak.

The *superior tibio-fibular joint* has anterior and posterior tibio-fibular ligaments, and dense fibres connect the head of the fibula to the capsule of the knee joint and external lateral ligament.

The *inferior tibio-fibular joint* has no well-defined ligaments. The bones are held firmly together, and the interosseous membrane of the leg, which is very narrow, forms part of both tibio-fibular joints. The lower end of the fibula is slightly on the anterior aspect of the lower end of the tibia.

*Ankle Joint*:—This joint has been studied by Achy (3) and Fick (26). The *anterior ligament* is a very thin membrane running from the lower border of the tibia to the upper border of the head of the astragalus. It does not cover a pad of fat as in Man. The *posterior ligament* runs between the adjacent borders of the tibia and astragalus. It also gains attachment to the lower end of the fibula, thus helping to complete the inferior tibio-fibular joint. It is very strong all over, and has no definite strengthening bands as in Man. The *external lateral ligament* consists of two parts corresponding to the anterior and median fasciculi of the tripartite ligament in Man. The short anterior part runs from the anterior border of the outer malleolus to the astragalus. The middle part consists of two very powerful bands running from the tip of the external malleolus to the outer side of the os calcis. Nothing corresponding to the posterior fasciculus in Man exists. The *internal lateral ligament* runs from the internal malleolus above to the scaphoid, astragalus, and os calcis below. It is not divisible into several bands as in Man, but there is one very thick band running from the malleolus to the inner aspect of the scaphoid bone.

*Intertarsal Joints*:—The tarsal bones form several joints and the ligaments are numerous. The *talo-calcanean joint* has the following ligaments:—1. Anterior, external, posterior, and internal talo-calcanean ligaments, which are just detected with difficulty. They close the joint on all sides. 2. The interosseous

talo-calcanean ligament is a strong bond of union between the bones. The *talo-calcaneo-navicular joint* has strong ligaments, but in this young animal they cannot be separated into special bands as in Man. The *calcaneo-cuboid joint* has a strong capsule, the strongest part being on the plantar aspect. External, inferior, internal, and dorsal ligaments are thickened parts of the capsule, but the internal one is hard to detect. The *long and short plantar ligaments* are absent in this young animal.

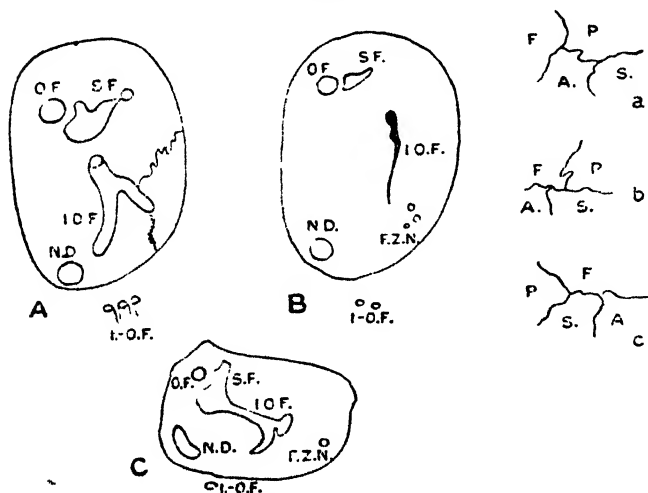
A dense fibrous mass covers the plantar aspect of the astragalo-scaphoid, scapho-cuboid, and cuneiform joints, but this cannot be divided into definite ligaments. The tendon of the peroneus longus is connected to this mass. A strong band runs from the scaphoid to the base of the first metatarsal bone, and this is the most obvious separate band.

The tarso-metatarsal, metatarso-phalangeal, and interphalangeal joints show nothing peculiar. They are built on the same general plan as in Man, but the individual ligaments are not so easily separated. The joint between the internal cuneiform and first metatarsal bones is very free.

*Note on the Pterion (text-fig. 13 A).*

As the skeleton has frequently been described and figured, no useful purpose is served to-day by descriptions of the bones of

Text-figure 13.



The bones of the orbit in the adult Orang (A), the very young Orang (B), and Man (C). The figures a, b, c represent variations in the pterion in the Orang. A., alisphenoid; F., frontal bone; I.O.F., infraorbital foramina; I.O.F., inferior orbital foramina; F.Z.N., foramina for zygomatic branches of the maxillary nerve; N.D., naso-lachrymal duct; O.F., optic foramen; P., parietal bone; S., squamosal; S.F., sphenoidal fissure.

single animals; but any special point should be noted. Various data are included above with the muscles and joints, so the present section is restricted to the pterion. It is usually stated that the parietal and alisphenoid articulate and separate the frontal and squamosal from one another. This is the case on both sides in an adult skull in my collection. In a skull of a young animal, which was changing from the milk to the permanent dentition, the frontal articulated with the squamosal to different degrees on each side. This skull (No. 49 A) is in the Museum of the Royal College of Surgeons of England. In no Orang skull have I yet seen a Wormian bone in the pterion such as there is in the skull of a young Chimpanzee in my possession.

#### ORGANS OF DIGESTION.

The *lips* are thick and protrude over the prognathous jaws. They are also very loose, and the animal converts the lower lip into a capacious trough during drinking. The frenula are short, and there is no philtrum. The mucosa is studded by the orifices of numerous glands. The *oral vestibule* can be made capacious; and its lining mucosa has numerous small papillæ besides the salivary papillæ. No large folds of mucous membrane are present, and there are no cheek-pouches.

*Tongue*:—In a former paper (70) I described the tongues of several animals, and I reviewed the literature. I pointed out that of all Primates the Orang resembles Man most closely in the lingual characters; there are no large conical papillæ on the base of the tongue, the vallate papillæ form a V, there are no frenal lamellæ, the plicæ are small, and the apical gland of Nuhn is present.

*Palate*:—The mucous membrane of the hard palate is bluish in colour. It has an elongated incisive eminence; and eight pairs of nodulated sinuous rugæ radiate from a median antero-posterior groove. Fick (26) points out that the rugæ in an old animal are not stronger than in an adult Man, but that is not the case in this young one. Beddard (6) and Gegenbaur (28) describe or figure the rugæ, and it appears that they vary in number and appearance in different animals. The soft palate has no uvula, and this is characteristic of all Orangs; all other Apes have a uvula. Many glandular orifices stud the mucosa of both hard and soft palates. The palate and oral mucosa are not pigmented.

*Œsophagus*:—The Œsophagus is entirely behind the trachea in the neck, as in the Chimpanzee. Its mucosa has a few transverse rugæ in the upper cervical division, but there are no rugæ in the lower part of the neck. On histological examination it is seen how there are two layers of muscles—an outer longitudinal layer, whose fibres are shown in text-fig. 6, and an inner circular layer. There is no trace of the third longitudinal

layer, which was seen by me in the Chimpanzee (72). The mucous membrane of the thoracic part of the œsophagus is totally devoid of rugæ.

The abdominal part of the œsophagus is short.

*The Stomach* (text-fig. 14).

The form differs from that in the Chimpanzee, Gorilla, and Man; but Flower (27) states that its appearance resembles that in the Chimpanzee. It has no fundus, the body has its long axis directed mainly proximo-distally, and the pyloric part is conical, with the long axis parallel to that of the œsophagus. The pyloric sphincter is very obvious when the stomach is passed between the fingers. About the middle of the body there is a well-marked notch on the greater curvature. The spleen is closely adherent to the greater curvature.

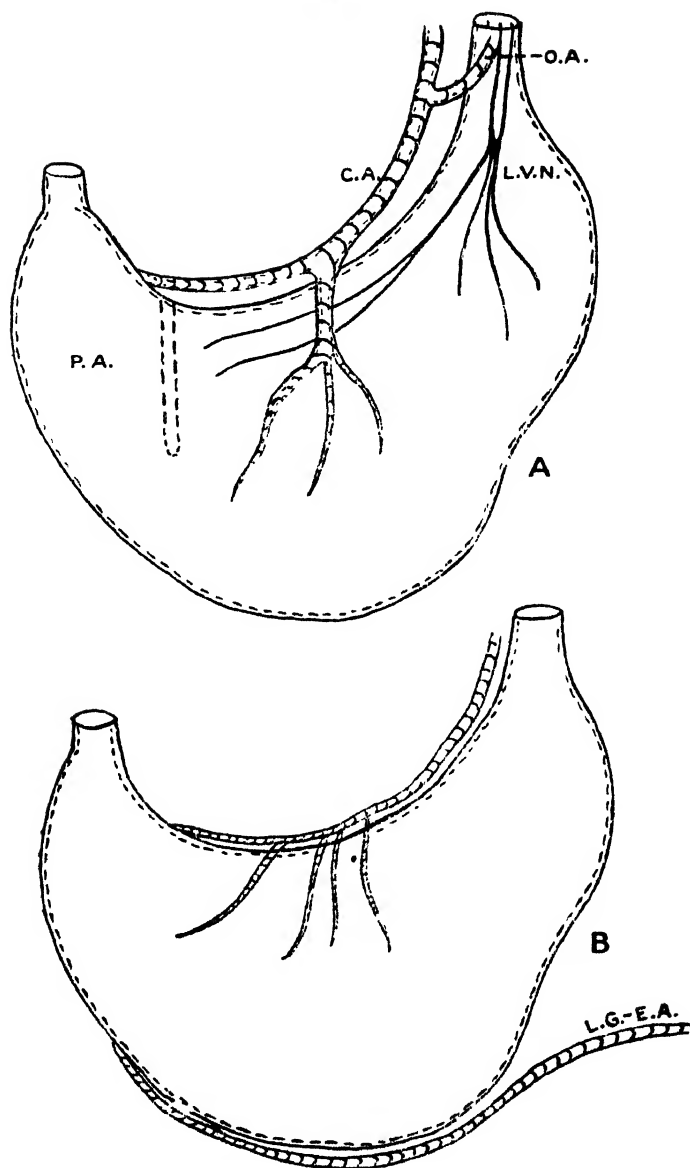
*Blood-supply*:—The coronary artery (C.A.) runs down between the layers of the lesser omentum. It gives off a well-marked œsophageal artery (O.A.), which passes upwards on the front of the abdominal part of the œsophagus and runs through the œsophageal opening in the diaphragm. As the parent stem runs downwards, it gives branches to both surfaces of the stomach, and one branch runs along the lesser curvature to the duodenum, where it anastomoses with the superior pancreatico-duodenal artery. The splenic artery gives off the left gastro-epiploic artery (L.G.-E.A.), which runs along the greater curvature between the two layers of the greater omentum. It supplies the dorsal surface of the stomach and anastomoses with the pyloro-duodenal arteries.

*Nerve-supply*:—The left vagus supplies the stomach by several branches (L.V.N.). These form a plexus, over the lower end of the œsophagus. From the plexus nerves pass to the anterior wall of the stomach, and others run along the lesser curvature as far as the pylorus. The right vagus gives branches to both walls of the stomach, and some run along the lesser curvature.

*Peritoneal Connections*:—The greater, lesser, and gastro-splenic omenta are similar to those in the Chimpanzee (72). The gastro-phrenic ligament is short, broad, and strong. The suspensory muscle of the duodenum was not seen.

When the stomach is opened along the greater curvature it is seen how the cavity is partially subdivided by a thick partition jutting down from the lesser curvature and connecting the ventral and dorsal walls of the stomach. It is continuous with the left wall of the pyloric antrum. The right or pyloric chamber is narrower than the left chamber, with which it communicates below the partition. The mucosa of the left chamber shows slight longitudinal folds, but it does not exhibit honeycomb-like depressions. The pyloric sphincter is a well-marked band. The very obvious pyloric antrum (P.A.) was previously described by Sandifort (65).

Text-figure 14.



The stomach from in front (A) and behind (B). Letters in text. The dotted line is the septum bounding the pyloric antrum.

*The Intestinal Tract.*

The *duodenum* describes the usual loop. It has no mesentery beyond the first part, which is ascending rather than horizontal. The hollow of the loop is small, but it lodges a piece of pancreas. The mucous membrane in this animal is quite smooth, but some authors describe numerous *valvulæ conniventes*. The biliary and pancreatic ducts open by a foramen, there being no bile papilla.

The *ileum* and *jejunum* vary in calibre in different parts, and the ileum passes horizontally into the *cæcum*. The mesenteric root runs as in Man, and it gives an attachment to a ligament which runs to the dorsal peritoneum over the end of the abdominal aorta; that ligament has a concave free edge pointing distally. The arterial supply comes from the superior mesenteric artery; the highest branch anastomoses with the left gastro-epiploic artery, and the lowest branch anastomoses with the ileo-colic branch of the superior mesenteric artery. These rami *intestini tenuis* subdivide more between the layers of the mesentery than do the corresponding vessels in the Chimpanzee. The mucous membrane is quite devoid of folds or ridges. The villi are all quite small, and no trace of Peyer's patches was observed. In the Chimpanzee there are four patches (72).

The ileum and jejunum together measure 13 feet.

The *cæcum*, which is two inches long, is conical in shape. The vermiform appendix hangs down from the back of its apex. The *cæcum* has no mesentery, but the appendix has a well-marked mesentery derived from the mesentery of the small intestines. In this animal the *cæcum* is the only part of the large intestine which is not thickly covered with fat. The ileum enters the *cæcum* close to the origin of the appendix, but the longitudinal muscle bands which sacculate the colon cannot be traced down to the appendix as in Man. The ileo-cæcal orifice is not protected by a valve resembling that in Man; the ileum projects into the *cæcum*, and its orifice lies under an archway of mucous membrane. The orifice of the appendix passes obliquely under a collar of mucous membrane. The appendix is 5·3 inches long.

The *ascending colon*, which is short and capacious, has no mesentery. It has a thick deposit of fat in this animal. The *transverse colon* has a long mesentery, and many appendices epiploicæ are attached to it. The *descending colon* is short and devoid of a mesentery; and the *iliac colon*, as in the Chimpanzee, has the longest mesentery. The ascending and descending colons are more capacious than the transverse and iliac colons. The *rectum* is straight throughout; it is provided with a mesentery right down to the pelvic floor, and numerous appendices epiploicæ are attached to its walls.

*Blood-supply of the Large Intestine*:—The gut from the *cæcum* to nearly the left end of the transverse colon is supplied successively by the ileo-colic, right colic, and middle colic branches



of the superior mesenteric artery. These vessels anastomose with one another, and the middle colic artery anastomoses with the left colic branch of the inferior mesenteric artery. The latter supplies the left end of the transverse colon, the descending colon, iliac colon, and rectum by its left colic, sigmoid, and hæmorrhoidal branches. All these arteries bifurcate, and the halves form the anastomoses in the usual way.

*Mucous Membrane of the Large Intestine:* - In the cæcum and colon the mucous membrane has a few longitudinal folds, but it is much simpler than in the Chimpanzee (72). The valves of Houston and Ball are absent. Well-marked longitudinal folds are at the lower end of the rectum.

The large intestine from the ileo-cæcal valve to the beginning of the rectum is 4 feet long, and the rectum is 4·6 inches long.

Bischoff (7), Broca (9), Flower (27), Mayer (49), and Hartmann (34) have described the characters or dimensions of different parts of the intestinal tract, and Herrmann (37) has dealt with the histology of the anal mucous membrane.

### *Salivary Glands.*

The *parotid gland* (text-fig. 2, P.G.) is very large. The base is wrapped round the lower border of the auricle, and the apex lies behind the angle of the jaw on the sterno-mastoid muscle. It is in contact below with the large submaxillary gland. Its component lobules vary in size, and several glands lie on the surface. Histological examination shows that these are true lymphatic glands. The duct (S.D.) crosses the masseter and suctorial pad of fat. It pierces the upper part of the buccinator muscle.

The gland covers more of the masseter than in the Chimpanzee.

The *submaxillary gland* (text-fig. 4) on each side is a globular body measuring an inch and a quarter in diameter. The two glands do not touch in the middle line. The duct has the usual course. It opens on a papilla and not on a frenal lamella.

The *sublingual glands* lie in the usual position. They are thin and triangular in shape, and their relations are as in the Chimpanzee. The ducts open into the anterior part of the floor of the mouth.

### *The Pancreas.*

The general characters and appearance are as in the Chimpanzee. The organ is deep black in colour and lobulated. It is also thin and flat. It is divided into the usual head, body, and tail; but no process runs up alongside the portal vein towards the liver. It receives its blood-supply from the hepatic and splenic arteries and from the celiac axis itself. The duct unites with the common bile-duct. The relations to the peritoneum are as in Man. The portal vein is formed within it in the usual way, although the pancreas is very thin.

### The Liver

The liver is divided into two lobes without any trace of lateral fissures. The fossa of the gall-bladder divides the organ into two nearly equal parts. The umbilical fissure is bridged over by hepatic tissue, and is concealed in consequence. The left lobe is smaller than in *Anthropopithecus* and *Hylobates*, and is not more than one-fourth of the organ. The fissure of the vena cava is superficial. The Spigelian lobe is prominent and subcylindrical, partly free on the left, and overlapping the portal fissure. The caudate lobe is partly free at its right extremity, which reaches nearly to the right margin of the gland. The gall-bladder, which is elongately pyriform, projects ventrally a short way beyond the free margin of the gland. Details of the structure of the liver are given by Barkow (4), Broca (9), Camper (11), Chapman (12), Fick (26), Flower (27), and Sandifort (65). In a hitherto unpublished note Garrod points out that the liver varies in individuals in the degree of bridging of the umbilical fissure, the position of the fissure of the vena cava, and the prominence of the caudate lobe. Using his method of expressing the characters of the liver, we get the following formulæ:—

<i>Simia</i> ..	R3 > L8 > Sp.
<i>Hylobates</i> ..	R > L > Sp. > C.
<i>Anthropopithecus</i> ..	R2 > L > Sp. = C.

In the Gorilla, as is well known from the writings of many authors, the liver presents primitive characters in the form of fissures, which are absent in the other Anthropoid Apes.

### The Peritoneum.

From observations made on this animal and from the account of Chapman (12), it is evident that the characters are similar to those which I have already described in the Chimpanzee (72).

### THE BLOOD.

Gulliver (32) pointed out that the red blood-corpuscles measure in diameter as follows:—

<i>Homo</i> ..	1/3200 inch.
<i>Simia troglodytes</i> .....	1/3412 „
<i>Pithecus satyrus</i> ..	1/3383 „
<i>Hylobates hoolock</i> ..	1/3368 „
„ <i>leucogenys</i> ..	1/3425 „
„ <i>rafflesii</i> ..	1/3589 „

There is thus a gradual increase from the Gibbons up to Man. Nuttall has shown that the blood of the Orang gives positive precipitative reactions of differing degrees of intensity with the blood of the other Anthropoid Apes and Man.

## ORGANS OF CIRCULATION.

The *pericardium* adheres extensively to the diaphragm. In this very young animal it is concealed, except for a very narrow rim close to the diaphragm, by the thymus gland (text-fig. 22).

The *heart* (Pls. I. & II.) is 2 inches long from the root of the pulmonary artery to the apex, 2 inches wide across the ventricular base, and  $1\frac{1}{2}$  inches ventro-dorsally at the ventricular base. It has the same form as in Man, and the apex lies behind the inner end of the fifth costal cartilage. The auricular appendages are small, particularly the left one; and the right appendix stretches in a tongue-like manner across the front of the ascending aorta. *Right Auricle*:—The interior is much as in Man. The *musculi pectinati* in the appendix and anterior wall are very numerous and end above in a well-marked *crista terminalis*. The Eustachian valve is very rudimentary, and the coronary valve is likewise poor and incompetent. The *fossa ovalis* is quite closed; it is bounded by a well-marked *limbus*. No trace of the *foramen ovale* exists. No distinct tubercle of Lower could be distinguished. The endocardium of the *vena cavæ* and *musculi pectinati* is darker than in the rest of the auricle. *Right Ventricle*:—The body of the ventricle and the *conus arteriosus* are not separated from one another by a muscular ridge, but papillary muscles cross the communication between them. The *conus* and body run down side by side in the ventricle as in Man, but the *conus* is mostly superior in the Chimpanzee. In Man and the Chimpanzee the lining of the *conus* is smooth, but it has *columnæ carneæ* of different kinds. The papillary muscles arise from an interlacing mass of muscle bundles on the right ventricular wall, and run separately to the cusps of the tricuspid valve. Several muscle bundles connect the right wall to the interventricular septum. Some *chordæ tendineæ* arise from the septum. In the Chimpanzee three papillary muscles form a strong bundle running to the valve, and some very powerful muscles connect the septum and right wall. The interventricular septum had one large and one small orifice (Pls. I. A & II. A) bringing the ventricles into communication in this animal. The significance of this occurrence is described on p. 445. The pulmonary valve is not peculiar. *Left Auricle*:—The appendix is occupied by *musculi pectinati*, and there is nothing to show the position of the *fossa ovalis* of the right auricle.

*Left Ventricle*:—The walls have *columnæ carneæ* lying on their surfaces. A few very small bundles run from the left wall to the interventricular septum. The long *chordæ tendineæ* to the mitral valve come from flat papillary muscles on the left wall. The aortic vestibule is not as smooth as in the Chimpanzee. Sandifort (65), Fick (26), and Chapman (12) describe the form and size of the heart, and Ruge (63) deals with its position.

*The Arteries.*

All accounts of the arteries are fragmentary, so the following detailed description will fill a gap in our knowledge of the anatomy of the Orang.

The *pulmonary artery* has the same course and relations as in Man. The right artery divided into three branches.

The *aorta* is relatively wider than in the Chimpanzee. It passes through the diaphragm at the level of the eleventh dorsal vertebra. It ends by dividing into the two common iliac arteries at the lower part of the body of the last lumbar vertebra. It decreases gradually in calibre till the superior mesenteric artery is given off, after which it suddenly becomes small. The branches are fewer than in Man, for there are two branches only from the arch, the phrenic arteries come from the coeliac axis, there are no suprarenal arteries, and the middle sacral artery is absent. The ductus arteriosus is closed. The branches differ in several ways from those which I have already recorded in my paper on the Chimpanzee; they are slightly more numerous in the Orang.

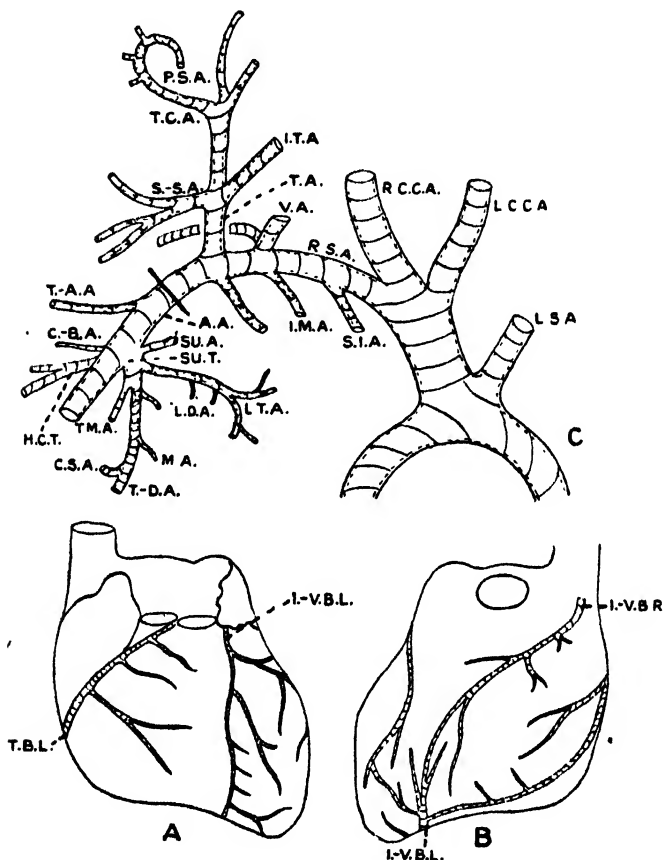
The *aortic arch* (text-fig. 15 C) describes the curve, and gives off the innominate and left subclavian arteries from its summit. The positions are not absolutely identical with any of those described and figured by Keith (44). In no Orang hitherto examined have the vessels been seen to arise as in Man, the Gorilla, and some Chimpanzees. The closure of the ductus arteriosus in this very young animal is against Deniker's view that it remains open till the end of the milk dentition (18).

The *coronary arteries* (text-fig. 15 A & B) arise from sinuses as in Man. The left one divides into transverse and interventricular branches. The interventricular branch runs down the anterior surface of the ventricles, turns round the right border, and ascends far on the posterior surface of the heart. It ends by anastomosing with the interventricular branch of the right coronary artery. It supplies the anterior surface of the left ventricle, and the posterior surfaces of both ventricles. The transverse branch supplies both surfaces and the left border of the left ventricle. The right coronary artery courses as in Man, and it likewise divides into transverse and interventricular branches. The transverse branch is minute, but I could not trace it to anastomose with the transverse branch of the left coronary artery. The interventricular branch anastomoses with the interventricular branch of the left coronary artery. It supplies the right ventricle. Small branches supply the front of the ventricle, and a marginal branch, which anastomoses with a branch of the left coronary artery, is well marked. Each coronary artery supplies an auricle and the coats of the aorta and pulmonary artery.

The *innominate artery* (text-fig. 15 C, I.A.) gives off the left common carotid artery (L.C.C.A.) and divides into the right

common carotid (R.C.C.A.) and right subclavian (R.S.A.) arteries. The left common carotid artery arises higher up than in any of Keith's specimens. It does not give off any thyroidea ima artery

Text-figure 15.



The heart from in front (A) and behind (B). C, the aortic arch and its main branches. I-V.B.L. and I-V.B.R., interventricular branches of the left and right coronary arteries; T.B.L., transverse branch of the left coronary artery; A.A., axillary artery (the thick line separates it from the right subclavian artery); the transverse branch of the vertebral artery (V.A.) is described in the text as the muscular artery (M.A.). Other letters in text.

such as I observed in three Chimpanzees. The *left subclavian artery* (L.S.A.) arises from the aortic arch very close to the innominate artery. In two Chimpanzees the arch gave off two

arteries as in this animal, but in one animal there were three branches as in Man. In eleven Chimpanzees, Keith found two branches arising from the arch; in seven animals the branches were as in Man. In nine Gorillas, only one animal departed from Man in the arrangement of these branches, and Deniker (18) came to similar conclusions. In the Gibbons the human arrangement does not exist. The course of the branches in the head and neck is given on page 401, and that in the human arm on page 403.

*Intercostal Arteries* :—Eleven pairs of small intercostal arteries are given off by the descending thoracic aorta. There is no large intercostal artery to the first space as Eisler described in the Gorilla.

The descending thoracic aorta also gives off œsophageal and left bronchial arteries. No right bronchial branch was detected. The œsophageal branches anastomose with the well-marked œsophageal branch of the coronary branch of the celiac axis, which ascends through the œsophageal opening in the diaphragm.

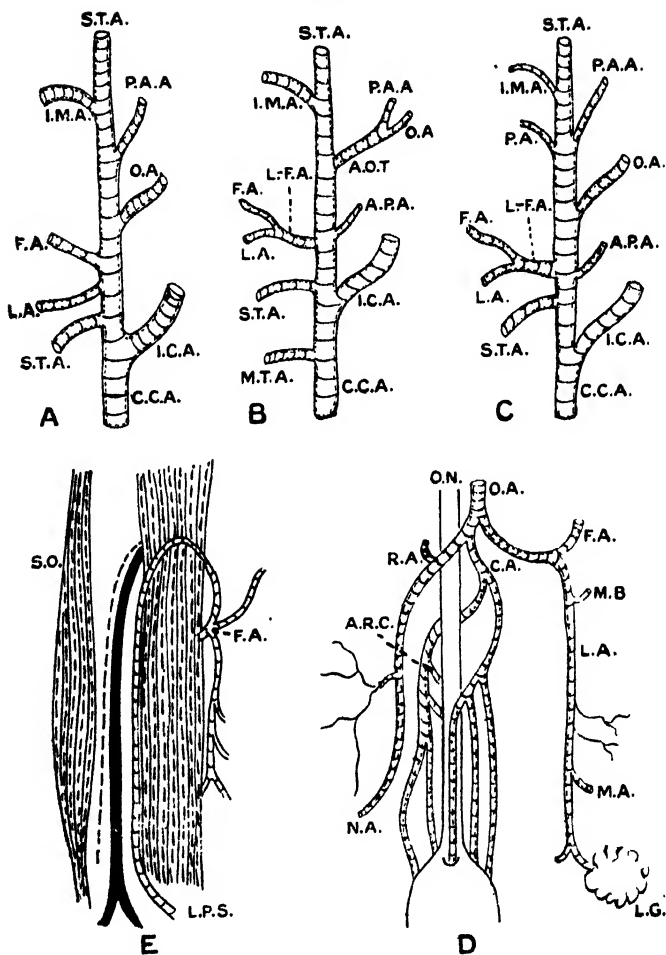
The aortic orifice in the diaphragm transmits the aorta and thoracic duct. It does not transmit the vena azygos major as in Man. The calibre of the thoracic aorta is wider than that of the abdominal aorta after the latter has given off the celiac axis and superior mesenteric artery. The calibre is relatively wider than in the Chimpanzee.

#### *Arteries of the Head and Neck.*

The common carotid arteries have the same origin, course, and relations as in the Chimpanzee, but no branches are present in this animal. In the Chimpanzee and Gorilla thyroid branches are given off. In one Chimpanzee it gave off superior, middle, and inferior thyroid arteries, in a second animal it gave off a superior thyroid artery, but it gave off no thyroid vessels in a third animal. Eisler (25) described thyroid branches of the common carotid in the Gorilla. In many lower Mammals the common carotid gives off thyroid arteries.

The external carotid artery (text-fig. 16 A-C) is encircled close to its origin by the hypoglossal nerve, and the descendens hypoglossi is given off on the front of the artery. It gives off the following branches: superior thyroid (S.T.A.), linguo-facial (L.F.A.), parotid (P.A.), internal maxillary (I.M.A.), superficial temporal (S.T.A.), posterior auricular (P.A.A.), occipital (O.A.), ascending pharyngeal (A.P.A.). It agrees with the other Catarrhini, except Man, in the possession of a linguo-facial trunk, and it differs from them and agrees with him in the separation of the occipital and posterior auricular arteries. It differs from all other Catarrhini, including Man, in the presence of a large parotid branch. There is no special ascending palatine artery as in the Gorilla.

Text-figure 16.



Arteries of the head and neck. A, B, and C, the carotid system in Man, the Chimpanzee, and the Orang respectively. D and E, the ophthalmic artery in the Orang. A.O.T., auriculo-occipital trunk; F.A., facial or frontal artery; C.C.A. and I.C.A., common and internal carotid arteries; L.A., lingual artery; L.G., lachrymal gland; L.P.S., levator palpebræ superioris; O.A., occipital artery; S.O., superior oblique muscle. Other letters in text.

The *linguo-facial trunk* breaks up into lingual and facial arteries. It has no other branches.

The *lingual artery* has the same course and relations as in the Chimpanzee, and it gives off the supra-hyoid, dorsalis linguæ, and several lingual branches whose distributions are similar.

The *facial artery* runs forwards and upwards under cover of the submaxillary gland, to which it sends branches. And it crosses the mandible and gets into the face at the anterior border of the masseter. In the face it first runs obliquely forwards and upwards to the angle of the mouth, where it disappears beneath the levator anguli oris; in the lower part of the face (text-fig. 2, F.A.) it gives a single inferior labial artery to the muscles of the lower lip. It then passes horizontally in the superficial part of the orbicularis oris in the upper lip, after giving off a small vessel, which ascends in the substance of the levator anguli oris. It ends by dividing into two vessels, which supply the upper lip.

The *superior thyroid artery* describes the usual downward course. It gives branches to the thyroid gland, the muscles attached to the hyoid bone, the fat and glands in the neck, and the hyoid musculature. Its mode of distribution differs slightly from that in the Chimpanzee.

The *occipital artery* courses in general as in the Chimpanzee (72). The main difference between it and the artery in the Chimpanzee is that it arises separately from the posterior auricular artery. In all other Apes there is an occipito-auricular trunk. In Man there is sometimes an occipito-auricular trunk, and sometimes the two vessels are separate. The Orang approaches Man more closely than do the other Apes in the characters of these vessels.

The *ascending pharyngeal artery* differs somewhat from the corresponding vessel in the Chimpanzee. It runs perpendicularly upwards, giving off pharyngeal branches. It bends forwards and ends in branches to the palate, palato-pharyngeus, and pharynx. And it gives off a meningeal artery. In the Chimpanzee it ends as a meningeal artery. In the Gorilla it is accompanied by an ascending palatine artery.

The *superficial temporal artery* is a short, stout artery. It runs vertically upwards for half-an-inch and, after giving off small parotid arteries, it divides into two branches. One runs directly upwards in front of the auricle, but the other runs forwards and upwards into the scalp. The parent stem is relatively longer in all other Anthropoids.

The *internal maxillary artery* (text-fig. 3) describes a curve and passes behind the neck of the mandible. In the pterygoid region it is first horizontal and then inclines upwards. It disappears through the sphenomaxillary fissure. It gives off the following branches:—

1. Two *deep temporal arteries* (D.T.A.). The anterior vessel is smaller and more horizontal than the posterior one. They anastomose in the temporal muscle.

2. Arteries to the suctorial pad of fat (S.P.F.).



3. Muscular arteries to the buccinator (B.A.), masseter (M.A.), and pterygoid (P.A.) muscles.
4. Inferior dental artery (I.D.A.).
5. Posterior superior dental artery (P.S.D.A.).
6. Mid meningeal artery.

After passing through the spheno-maxillary fissure the artery turns upwards, and is later continued as the *spheno-palatine artery* through the spheno-palatine foramen into the nasal cavity. It gives off the following branches from the fissure to the nose:—

1. Descending palatine artery to the mucosa of the mouth, soft palate, and gums. It has numerous branches.
2. Pterygo-palatine artery to the roof of the pharynx.
3. Infra-orbital artery. This vessel is not seen from the orbit in this animal, as no inferior orbital groove exists. It passes forwards along with the infra-orbital branches of the trigeminal nerve, and ends by supplying the skin of the cheek.
4. Naso-palatine arteries to the nose, soft palate, and pharynx. These come from the spheno-palatine artery.

I was unable to detect any trace whatsoever of the Vidian artery.

The *Internal Carotid Artery* as in the Chimpanzee and Man.

The *ophthalmic artery* (text-fig. 16 D & E) enters the orbit on the outer side of the optic nerve, and it may cross over its upper surface to its inner side as in Man. After a short course it gives off a *ciliary artery* (C.A.), which divides into posterior ciliary vessels; these run along the sides of the optic nerve, and one gives off the *arteria retinæ centralis* (A.R.C.), which passes into the inner side of the optic nerve (O.N.). A little farther forwards the parent stem gives off the *recurrent artery* (R.A.), which passes backwards to supply the dura mater in the middle cranial fossa. A large lachrymo-frontal artery arises from the left artery, but the right artery gives off a lachrymal artery. The lachrymo-frontal artery runs laterally and divides into lachrymal and frontal arteries, which diverge at right angles. The *frontal artery* (F.A.) describes a posterior curve and runs forwards on the upper surface of the levator palpebræ superioris (text-fig. 16 E), and it ends as in Man. The *lachrymal artery* (L.A.) runs forwards to supply the lachrymal gland, external and superior recti, and upper eyelid. Branches also accompany the temporo-malar nerve. I could not trace any anterior ciliary arteries as in Man. A well-marked meningeal branch (M.B.) runs back from the lachrymal artery to the middle cranial fossa, and a small artery (M.A.) passes through the orbital roof to the anterior fossa. The ophthalmic artery is continued into a *nasal artery* (N.A.), which supplies the skin of the outer nose and eyelids. It also gives off a branch, which supplies the tissues of the orbit and the sheath of the optic nerve; it also gives off ciliary arteries.

A peculiar feature of the eye is the small size of the globe, the large number of posterior ciliary arteries, and the absence of anterior ciliary arteries; and this will be investigated histologically when fresh material becomes available.

The *ophthalmic veins* run much as in Man.

### *Arteries of the Thoracic Wall and Arm.*

The *Subclavian Arteries* (text-fig. 15 C) have the same course and relations as in other Primates. The branches differ from those in three Chimpanzees examined by myself, and from those in the Gorilla recorded by Eisler (25). The main branches are the vertebral, thyroid axis, internal mammary, superior intercostal, and thymic arteries. They are therefore similar to those in Man except for the last-mentioned branch.

The *internal mammary artery* (I.M.A.) runs as in Man. It divides into superior epigastric and musculo-phrenic arteries in the fifth intercostal space. It gives off thymic and mediastinal arteries, and a minute intercostal vessel arises in each space.

The *superior intercostal artery* (S.I.A.) crosses over the first rib and enters the thorax. It supplies the first two intercostal spaces.

The *vertebral artery* (V.A.) is the largest branch. It enters the foramen in the transverse process of the sixth cervical vertebra along with filaments from the inferior cervical sympathetic ganglion. A large vertebral vein emerges behind it. It gives off a large branch (M.A.) to the levator scapular and serratus magnus.

The *Thyroid Axis* (T.A.) ascends and divides into inferior thyroid, transverse cervical, and supra-scapular arteries. The *inferior thyroid artery* (I.T.A.) runs upwards and inwards, and ends in the lower part of the right thyroid lobe. It is absent on the left side. The *transverse cervical artery* (T.C.A.), after giving off small branches to the muscles in the posterior triangle, curves backwards under the trapezius above the scapula. It gives branches to the trapezius and deep cervical muscles, and turns down along the vertebral border of the scapula as the posterior scapular artery (P.S.A.). The *supra-scapular artery* (S.S.A.) courses as in the Chimpanzee and Man. It gives off acromial branches to the muscles in that region, the subscapular artery to the subscapularis, and supraspinous and infraspinous arteries to the corresponding muscles. The acromial branches and thoracic axis anastomose and supply the glands above the clavicle.

The *Axillary Artery* (text-fig. 15) divides into the following branches:—

1. *Thoracico-acromial Axis* (T-A.A.):—This vessel arises from the upper border of the axillary artery. It gives off pectoral and acromial arteries, and is continued as a deltoid artery.

2. *Muscular artery* (C-B.A.) to the origin of the coraco-brachialis.

3. *Circumflex Trunk* (H.C.T.):—This vessel is not combined with the subscapular trunk as it is in the Chimpanzee. It gives off a small anterior humeral circumflex, and is continued as a large posterior humeral circumflex artery. The former passes under the origin of the coraco-brachialis and divides into several vessels which supply the muscles inserted into the front of the head of the humerus. The latter passes back over the tendon of the latissimus dorsi, and divides into two vessels which supply the deltoid. I did not trace an actual anastomosis between the two circumflex arteries, nor did a vessel pass up behind the long head of the biceps to the shoulder joint.

4. *Subscapular Trunk* (Su.T.):—Small muscular arteries are given off to the subscapularis (Su.A.), teres major (T.M.A.), and latissimus dorsi (L.D.A.). The *long thoracic artery* (L.T.A.) also arises from the trunk; it gives off branches to the latissimus dorsi, and divides into two arteries which diverge and supply the lower part of the serratus magnus. The trunk runs down on the deep surface of the subscapularis, and passes between the adjacent borders of the teres major and long head of the triceps. It gives off a fine *muscular artery* (M.A.) to the teres major and latissimus dorsi. It ends by dividing into circumflex scapular (C.S.A.) and thoraco-dorsal (T-D.A.) arteries. The *circumflex scapular artery* supplies the supraspinatus and infraspinatus muscles, and the *thoraco-dorsal artery* ends in the latissimus dorsi at the inferior angle of the scapula. I traced no communication between the terminal branches and the descending branch of the transverse cervical artery; so there is no anastomosis round the scapula.

The *Brachial Artery* (text-fig. 17 A) is of considerable length. It extends from the lower border of the teres major to an inch distal to the internal epicondyle of the humerus. There it gives off the radial artery and is continued as the ulnar artery.

It gives off fewer branches in the arm than in the Chimpanzee. The branches are as follows:—

1. Muscular to the teres major, latissimus dorsi, and dorso-epitrochlearis (M 1).
2. Muscular to the triceps (M 2).
3. Muscular to the biceps and brachialis anticus (M 3).
4. Muscular arteries to the brachialis anticus (M 4).
5. Articular to the elbow joint (Artic.A.).

There is no definite anastomosis round the elbow joint.

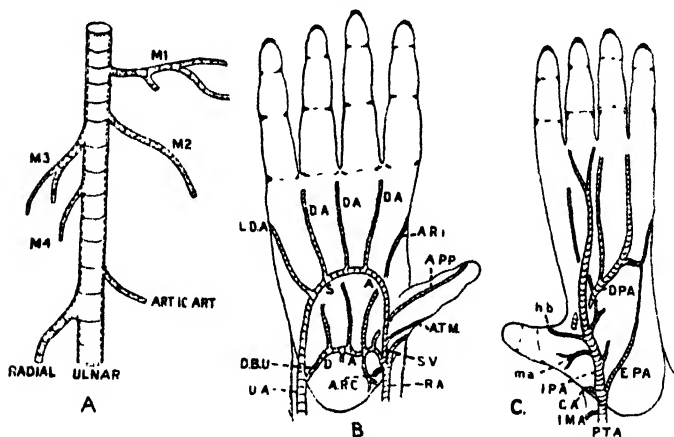
The *Radial Artery* (text-fig. 17 B, R.A.) runs distally. At a point an inch and a half above the carpus it gives off the superficialis volæ (S.V.). It then winds round the radial border of the carpus, runs under the extensor tendons, and passes forwards in the interval between the index and medius. It supplies the carpus and the muscles between the pollex and index. At the

junction of the parent stem and the superficialis volæ the anterior radial carpal (A.R.C.) is given off to the front and side of the carpus.

The *superficialis volæ* (text-fig. 17 B, S.V.) forms the superficial palmar arch with the ulnar artery. And the following branches are given off from the arch and the terminal parts of its constituent arteries:—1. Arteries to the thenar muscles (A.T.M.); 2. Princeps pollicis (A.P.P.), which arises in Man from the deep arch; 3. Digital arteries (D.A.) to the adjacent margins of the fingers; 4. An artery to the ulnar side of the minimus (L.D.A.); 5. A small artery to the tissues over the palmar aponeurosis. No digital arch is present similar to that which I observed in two out of three Chimpanzees.

The *Ulnar Artery* (text-fig. 17 B, U.A.) is the large continuation

Text-figure 17.



Arteries of the arm (A), hand (B), and foot (C). P.T.A., posterior tibial artery. Other letters in text.

of the brachial artery. It runs deep to the superficial flexor muscles and enters into the superficial palmar arch. It gives off the following branches:—1. Anterior interosseous artery; 2. Ulnar recurrent artery; 3. Muscular to the superficial flexor muscles; 4. Muscular vessels to the deep flexor muscles; 5. Anterior ulnar carpal; 6. Deep branch (D.B.U.).

The *anterior interosseous artery* runs down on the interosseous membrane. It passes behind the pronator quadratus and ends by anastomosing with twigs of the carpal arteries.

The *ulnar recurrent artery* runs up and supplies the elbow joint and muscles arising from the internal condyle of the humerus. It anastomoses with one of the muscular branches of the brachial artery behind the condyle.

The *anterior ulnar carpal artery* supplies the front and side of the carpus. It does not form an anterior carpal arch with the anterior radial carpal artery.

The *deep branch* (text-fig. 17 B) forms the main part of the deep palmar arch, which is continued into the *arteria radialis indicis* (A.R.I.).

It will be seen, on comparing the palmar arches of the Orang with those in the Chimpanzee (72) and Man, that Man and the Orang have both arches well developed; and there are only small differences in detail in the branches. In the Chimpanzee the deep arch is well developed, but the superficial arch is small. In the Gorilla there is no superficial arch at all, and Duckworth (20) and Manners Smith (69) think that is because the arm has not yet lost its function of acting as a support for the body.

Manners Smith has described the arteries of the fore-limb, and given the branches as follows:--

**Axillary Artery:**

1. Thoracic axis.
2. Branch to shoulder.
3. Subscapular.
4. Circumflex humeral giving off profunda brachii.

**Brachial Artery:**

1. Profunda brachii.
2. Superior ulnar collateral.
3. Inferior ulnar collateral.
4. Recurrent radial.
5. Recurrent interosseous.
6. Dorsal interosseous.
7. Palmar interosseous.

**Radial Artery:**

1. Ramus carpeus volaris.
2. Superficialis volæ.
3. Dorsalis pollicis.
4. Dorsalis indicis.
5. Metacarpea dorsalis.
6. Ramus carpeus dorsalis.

**Ulnar Artery:**

1. Deep branch.
2. Digital arteries from contribution to superficial palmar arch.

*Arteries of the Abdomen.*

The *Cœliac Axis* (text-fig. 18 A, C.Ax.) is a short, stout artery, which springs from the aorta between the crura of the diaphragm. It gives off the two inferior phrenic (I.P.A.), hepatic, splenic, coronary, and pancreatico-duodenal arteries. In Man



The *splenic artery* (S.A.) is not larger than the hepatic artery. It gives off pancreatico- and left gastro-epiploic arteries, and ends by dividing into three main splenic arteries, each of which subdivides into small vessels which enter the hilum of the spleen. The two pancreatic arteries (PANC.) arise from the splenic artery, and the left gastro-epiploic artery (L.G.-E.A.) is one of the main terminal divisions.

The *hepatic artery* (H.A.) is a long vessel. After giving off a pancreatico-duodenal artery it divides into right and left hepatic and cystic arteries (*rh.*, *l.h.*, *c.a.*). The pancreatico-duodenal artery (P.D.A.) supplies the head of the pancreas, pylorus, and duodenum; it anastomoses with branches of the celiac axis, splenic and superior mesenteric arteries.

The *pancreatico-duodenal artery* (P.D.B.C.) supplies the pancreas and duodenum and anastomoses with branches of the hepatic, splenic, and superior mesenteric arteries. There is thus an intricate arrangement of arteries round the pyloro-duodenal junction.

The *inferior phrenic arteries* (I.P.A.) are large vessels. They cross the crura of the diaphragm and are distributed much as in Man. In the Chimpanzee a single phrenic branch of the abdominal aorta bifurcates into two inferior phrenic arteries.

The *Superior Mesenteric Artery* arises from the aorta close to the celiac axis. It sweeps down into the right iliac fossa, and describes a curve with the convexity to the left. It gives off the following branches:—

*Rami intestini tenuis*:—These vessels form the usual arcades between the layers of the mesentery. The highest one enters into an anastomosis with branches of the hepatic and splenic arteries and the celiac axis. The lowest one anastomoses with a branch of the ileo-colic artery.

The *ileo-colic artery* is the largest branch of the superior mesenteric artery. Its branches anastomose with the rami intestini tenuis on the one hand, and a branch of the right colic artery on the other. It sends off a well-marked artery to the vermiform appendix.

The *mid-colic artery* arises in common with the last artery. Its terminal branches anastomose with the ileo-colic branch of the superior mesenteric artery and a branch of the left colic branch of the inferior mesenteric artery.

The superior mesenteric artery supplies the gut from the duodenum to the beginning of the splenic flexure of the colon. It is accompanied by branches of the vagus and sympathetic nerves (see p. 429).

*Renal Arteries*:—Both arteries arise from opposite sides of the aorta at the same level. They supply the suprarenal capsules, renal capsules, and kidneys.

*Ovarian Arteries*:—The left ovarian artery arises from the inferior mesenteric artery, whereas the right one arises from the abdominal aorta.

*Inferior Mesenteric Artery*:—This vessel gives off a small, tortuous left renal artery, and divides into upper and lower branches. The upper branch, or *left colic artery*, divides in the usual manner, and the branches anastomose with the middle colic artery and with the sigmoid branch of the inferior mesenteric artery. The lower branch divides into a *large sigmoid artery*, and a small *superior hæmorrhoidal artery* which descends into the pelvis. Branches of the sigmoid artery anastomose with one another and with the branches of the left colic and superior hæmorrhoidal arteries.

*Lumbar Arteries*:—Three pairs of lumbar arteries and one unpaired artery arise from the abdominal aorta. The unpaired vessel, which is the lowest as well, divides into two lumbar arteries and gives off a trunk, which divides into the middle and two lateral sacral arteries.

The *Common Iliac Arteries* are each an inch and a half long. They have no branches, and they divide in the usual way at the lower border of the sacro-iliac joints.

The *External Iliac Artery* (text-fig. 18 B, E.I.A.) has the same course as in the other Apes and in Man. It gives off the following branches:—

1. The *deep epigastric artery* (D.E.A.) gives branches to all the muscles of the anterior abdominal wall. It anastomoses with branches of the deep circumflex iliac, lumbar, and superior epigastric arteries.

2. The *deep circumflex iliac artery* (D.C.I.A.) curves laterally and runs up between the transversalis and internal oblique muscles, to which it gives branches.

3. A vessel (O.-I.C.A.) which combines the obturator and internal femoral circumflex arteries. It runs downwards over the pelvic brim, passes in a curve over the outer surface of the obturator externus muscle, and divides into transverse and descending branches. Several vessels arise from it. Within the abdominal cavity it gives off the *obturator artery*, (O.A.), which supplies the obturator internus, pubis, and pelvic lymph-glands. In the upper part of the thigh it gives off a *nutrient artery* (N.A.) to the pubis, and a *muscular artery* (M.A.) to the obturator externus and adductor brevis. On the widest part of its curve it gives off a large *adductor artery* (A.A.), which supplies the upper part of all the muscles forming the adductor group. The *descending terminal branch* (D.T.B.) ends in the adductor magnus, and the *transverse terminal branch* (T.T.B.) supplies the hamstring muscles and quadratus femoris. No direct anastomosis was observed between it and the gluteal arteries.

The *Femoral Artery* first gives off a superficial circumflex artery (S.C.A.) which courses as in Man; and also supplies the ilio-psoas and sartorius. No genital or epigastric artery comes from the femoral artery. The parent stem gives off the profunda femoris and continues as the superficial femoral artery. The



latter gives off the saphenous artery and passes between two parts of the adductor magnus, after which it becomes the popliteal artery.

The *saphenous artery* runs down to the foot and becomes the *dorsalis pedis*. It gives a small branch to the hallux and a large one to the second interspace; from the latter small branches go to the tissues on the dorsum of the foot. The parent stem then dips deeply between the hallux and second digit and plays the chief part in supplying the sole of the foot.

The *profunda femora* (P.F.A.) gives off a muscular artery (*m.a.*) to the sartorius and quadriceps extensor. More distally it gives off the lateral femoral circumflex artery (L.F.C.A.) and ends in the adductor magnus. No perforating arteries exist, so the Orang agrees with the Chimpanzee and differs from Man.

The *lateral femoral circumflex artery* (L.F.C.A.) passes outwards round the back of the femur, and appears superficially after passing over the hamstring muscles. It ends by dividing into ascending, transverse, and descending branches. The ramifications of the branches had been torn away in the removal of the skin.

The *Popliteal Artery* differs from that described in my paper on the Chimpanzee. It is a long vessel, which gives off the following branches:—

1. A muscular artery to the quadriceps extensor and adductor magnus. This vessel is only present on the right side.
2. Two geniculate vessels to the knee.
3. Peroneal artery, which ends in the skin on the outer side of the heel. It also supplies the posterior tibial muscles high up.
4. Muscular artery to the upper part of the gastrocnemius.

At the lower border of the popliteus the popliteal artery divides into anterior and posterior tibial arteries.

The *Anterior Tibial Artery* almost immediately after its formation gives off a muscular artery to the flexor digitorum tibialis posticus. It then passes downwards and forwards between the tibia and fibula. As soon as it reaches the anterior tibial region it gives off a recurrent artery to the tissues over the front and sides of the head of the tibia. Then it divides into two branches. One runs superficially and supplies the three anterior tibial muscles. The other runs down on the interosseous membrane, gives a nutrient artery to the fibula, and supplies the malleoli and ankle joint.

The *Posterior Tibial Artery* (text-fig. 17 C) runs as in Man. It divides into a large internal (I.P.A.) and a small external plantar artery (E.P.A.). It gives off the following branches:—

1. Muscular twigs to all posterior tibial muscles.
2. Internal malleolar artery (I.M.A.).

The *internal plantar artery* is the continuation of the posterior tibial artery. It passes distally on the surface of the plantar

fascia (text-fig. 17 C, I.P.A.). It gives off a large artery to the outer surface of the hallux (*h.b.*), a calcanean artery (*c.a.*) to the heel, a muscular artery (*m.a.*) to the adductor hallucis, and digital arteries to the adjacent sides of the second, third, and fourth digits.

The *external plantar artery* (text-fig. 17 C, E.P.A.) passes distally and laterally, diminishing rapidly in size, till it unites with the continuation of the *dorsalis pedis* artery.

The *dorsalis pedis* (D.P.A.) forms a plantar arch from the interval between the hallux and index to the fourth interdigital space (text-fig. 17 C). There it receives the external plantar artery and runs distally to the outer side of the fifth digit. It gives branches to the inner side of the second digit and the clefts between digits 2-5. Recurrent branches run to the tarsal joints.

The *Internal Iliac Artery* (text-fig. 18 B, I.I.A.) soon divides into two parts, whose branches are as follows:—

#### A. Anterior Division.

1. Utero-vesical artery (U-V.A.).
  - a. Vesical twigs (*ve.b.*).
  - b. Uterine twigs (*u.b.*).
  - c. Vaginal twigs (*v.b.*).
2. A gluteal trunk, which divides into:
  - a. Superior gluteal artery (S.G.A.).
  - b. Inferior gluteal artery (I.G.A.).
3. Obliterated hypogastric artery (O.H.A.)

#### B. Posterior Division which gives off:

1. Lateral sacral artery (L.S.A.).
2. Pudendal artery (P.A.).

These branches differ in their origins from those in the Chimpanzee (72), and approximate to those in Man.

The *utero-vesical artery* divides into upper and lower branches. The former is the superior vesical artery. The latter divides into middle vesical and uterine arteries; and the uterine artery gives off uterine, vaginal, and inferior vesical twigs. The vessels run in the organs as in the Chimpanzee.

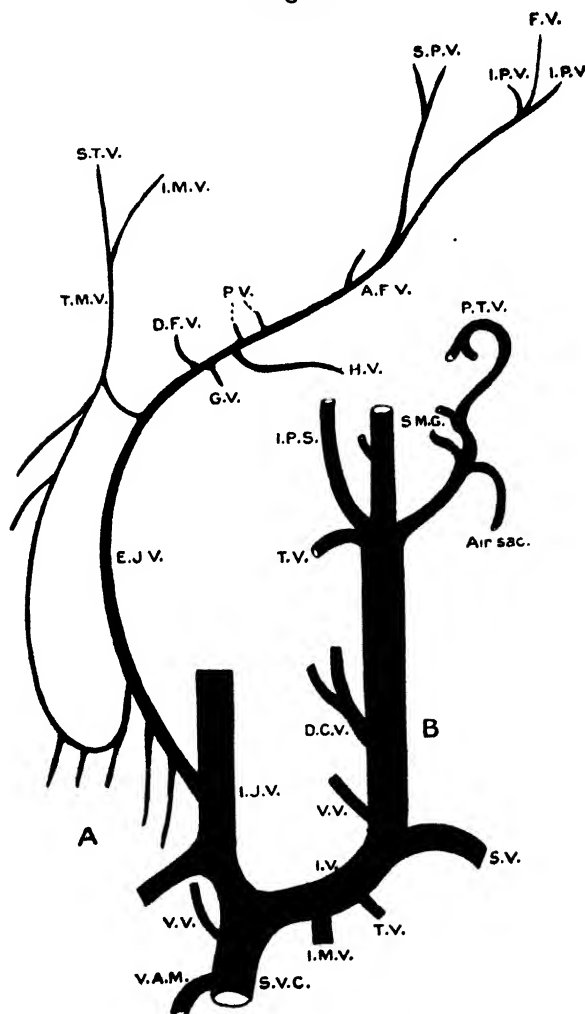
The *superior gluteal artery* emerges from the pelvis above the pyriformis. It breaks up into twigs to the gluteus medius, gluteus minimus, and scansorius. It is accompanied by the superior gluteal nerve. The *inferior gluteal artery* emerges along with several nerves below the pyriformis, and supplies the gluteus maximus. No extra-muscular anastomoses were seen between the gluteal and circumflex vessels.

The *obliterated hypogastric artery* was only present on the right side.

The *pudendal artery* runs infero-laterally and divides into two branches. One branch runs upwards and forwards, and gains

entrance to the perineum by passing above the ischio-cavernosus muscle (text-fig. 10). It gives off the dorsal artery of the clitoris and ends in the tissues of the labia. The other branch becomes

Text-figure 19.



Veins of the head, neck, and upper part of the thorax. S.T.V., superficial temporal vein; I.M.V., internal maxillary vein. Other letters in text.

the inferior hæmorrhoidal artery, which supplies the gut, the levator ani, and sphincter ani externus. It is surrounded by much fat, and it does not pass through a well-defined Alcock's canal.

*Veins of the Head and Neck* (text-fig. 19).

The *anterior facial vein* (A.F.V.) begins at the inner canthus of the eye as the *frontal vein* (F.V.), which drains the forehead. It courses round the orbit, receiving *inferior palpebral veins* (I.P.V.) from the lower lid. On the malar bone it receives the *superior palpebral vein* (S.P.V.) from the upper eyelid. Then the anterior facial vein curves downwards and backwards and round the base of the parotid gland, from which it receives tributaries (P.V.). As it crosses the masseter below the parotid gland, it receives a large *hyoid vein* (H.V.) from the tissues overlying the hyoid bone, and a small *glandular vein* (G.V.) from the glands on the angle of the mandible. It also communicates with the pterygoid veins through the *deep facial vein* (D.F.V.). In the Chimpanzee the latter vein is situated high up in the face. The anterior facial vein unites with the anterior division of the *temporo-maxillary vein* (T.M.V.) to form the *external jugular vein* (E.J.V.), which runs downwards and backwards over the sterno-mastoid, turns round its posterior border, and ends in the *internal jugular vein* (I.J.V.). It receives tributaries from the glands and fat in the clavicular and delto-pectoral group. The arrangement of the external jugular vein described above differs considerably from that in three Chimpanzees examined by me. In them the vein passed deep to the sterno-mastoid muscle and received the internal jugular vein. Moreover, it was very large, whereas it is very small in the Orang. The posterior division of the temporo maxillary vein forms a loop with one of the tributaries of the external jugular vein.

No *anterior jugular vein* is present.

The *internal jugular vein* is very large, and drains a wide area, whereas in three Chimpanzees it was merely a short trunk connecting the lateral and inferior petrosal sinuses to the posterior facial vein. About the level of the hyoid bone it receives a large vein, which drains the tongue, submaxillary gland (S.M.G.), pharynx (P.V.), and pterygoid region (P.T.V.). The inferior petrosal sinus (I.P.S.) and thyroid veins (T.V.) enter it at the same place. At the root of the neck it receives the *external jugular vein* (E.J.V.), *deep cervical* (D.C.V.) and *vertebral veins* (V.V.). It unites with the subclavian vein to form the *innominate vein*.

*Veins of the Arm* (text-fig. 20 A).

The *superficial veins* differ from those in the Chimpanzee. From the veins on the dorsum of the hand the *cephalic vein* (C.V.) runs up on the dorsum of the forearm. Veins ascend from the thenar and hypothenar areas. The former bifurcates; one half winds round the radius and joins the cephalic vein; the other half unites with the hypothenar vein to form a vessel which joins the cephalic vein in the upper part of the forearm.

The humeral cephalic vein ascends in the lateral bicipital groove and, passing through the delto-pectoral triangle, it unites with the lateral vena comitans of the brachial artery. There is no basilic vein, and no cubital vein connects the superficial and deep veins.

The *deep veins* from the forearm form a plexus in front of the lower end of the brachial artery. From the plexus two venæ comites run up along the brachial artery. The lateral vena comitans receives the humeral cephalic vein; the median vena comitans receives the subscapular vein (S.V.), which receives circumflex, scapular, and thoracic veins; and the two venæ comites unite to form the axillary vein (A.V.), which becomes the subclavian vein later on.

#### *Veins of the Thorax* (text-fig. 19).

The *left innominate vein* (I.V.) is longer and more horizontal than the right one. It courses as usual and unites with the right vein (R.I.V.) to form the superior vena cava. It receives a thymic vein (T.V.) and the internal mammary vein (I.M.V.).

The *superior vena cava* (S.V.C.) is not peculiar. It receives the right vertebral vein (V.V.) and the vena azygos major (V.A.M.).

#### *Veins of the Leg.*

The arrangement of the superficial veins differs in some ways from that in the Chimpanzee. Three superficial veins arise from the dorsal venous arch on the foot. An inner vein runs up along the saphenous artery. Two outer veins ascend across the back of the leg, and they are united by a cross vessel. The saphena vein receives one of the outer veins and opens into the popliteal vein. The remaining outer vein ascends on the surface of Scarpa's triangle and ends in the femoral vein immediately below Poupart's ligament.

#### *Veins of the Abdomen* (text-fig. 20 B).

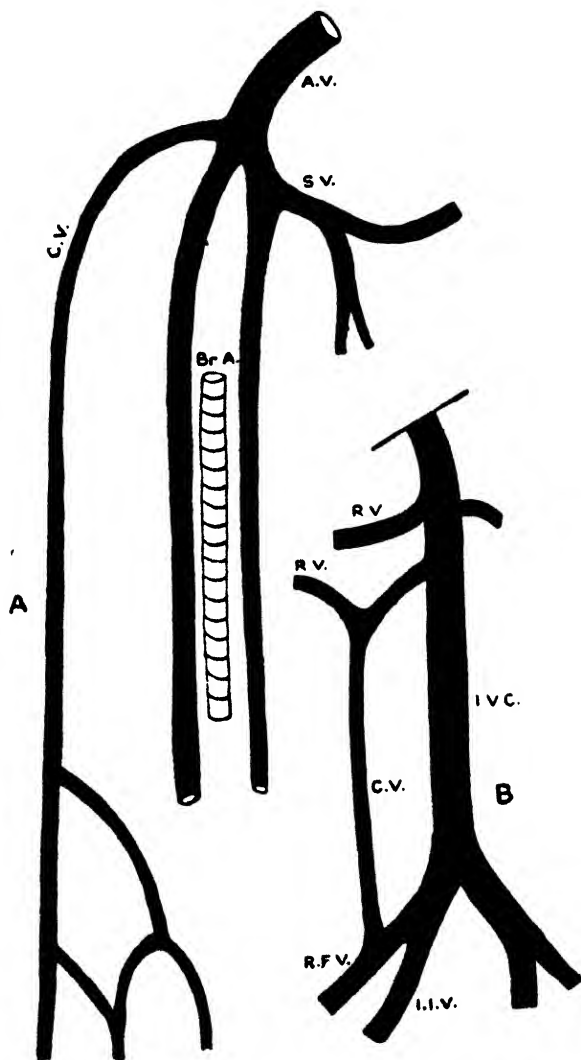
The right femoral vein (R.F.V.) becomes the right external iliac vein. The latter joins the internal iliac vein (I.I.V.) to form the common iliac vein (C.I.V.). It also sends up a large vessel (C.V.), which receives a vein from the right kidney and opens into the inferior vena cava (I.V.C.). The left external iliac vein unites in the usual way with the left internal iliac vein to form the left common iliac vein, but it does not send any vessel upwards as in the case of the right vein.

The inferior vena cava ascends on the left side of the abdominal aorta. In the upper part of the abdomen it crosses the aorta and ends in the liver. It receives both renal veins and the vessel ascending from the right external iliac veins. Two lumbar veins open into its posterior aspect.

The most interesting feature in the abdominal veins is the arrangement of the renal veins (R.V.) on the right side. One vein opens directly into the vena cava, and another unites with a

vein from the right external iliac vein to form a trunk which enters the vena cava.

Text-figure 20.



Veins of the arm (A) and abdomen (B). Br.A., brachial artery  
Other letters in text.

The internal iliac veins are arranged similarly to the branches of the internal iliac artery (text-fig. 18 B).

## THE LYMPHATIC SYSTEM.

The *receptaculum chyli* is a thin-walled fusiform sac measuring .7 inch long and .1 inch wide, lying between the aorta and right crus of the diaphragm. Vessels enter its lower end and sides from the abdomen. The *thoracic duct* leaves the upper end. It is single throughout, and runs as in Man. Small lymph-vessels enter it obliquely or transversely. The lymphatic glands are fewer than in Man, as is shown in the following table:—

GLANDS.	MAN.	ORANG.	CHIMPANZEE.
<i>Head and neck.</i>			
Occipital .....	+	0	+
Mastoid .....	+	0	0
Internal maxillary .	+	.	0
Parotid .....	+	+	+
Buccal .....	+	+	+
Lingual .....	+	0	0
Superficial cervical	+	0	0
Submaxillary .....	+	+	+
Suprahyoid .....	+	0	+
Retropharyngeal .....	+	0	0
Prelaryngeal .....	+	0	0
Pretracheal .....	+	0	0
Deep cervical ...		.	One large group.
upper .....	+	+	
lower .....	+	+	
<i>Upper extremity.</i>			
Epitrochlear .....	+	0	0
External axillary ..	+	+	+
Pectoral .....	+	0	0
Subscapular .....	+	+	+
Infraclavicular ...	+	+	+
Delfto-pectoral .....	+	0	0
<i>Lower extremity.</i>			
Inguinal (2 sets) ....	+	+	+
Popliteal .....	+	+	0
Anterior tibial ...	+	0	0
Deep femoral .....	+	0	0
<i>Thorax.</i>			
Intercostal .....	+	+	0
Sternal .....	+	0	0
Diaphragmatic .....	+	0	0

GLANDS.	MAN.	ORANG.	CHIMPANZEE.
<i>Thorax.</i>			
Ant. mediastinal .....	+	0	0
Sup. mediastinal .....	+	+	0
Post. mediastinal .....	+	+	0
Bronchial .. .. .	+	+	+
<i>Abdomen.</i>			
Gastric .....	+	+	+
Splenic ... . .	+	0	0
Hepatic .. .. .	+	0	0
Pancreatic .....	+	0	0
Mesenteric .....	+	+	+
Ileo-colic.....	+	0	0
Appendicular . . . .	+	0	0
Colic .....	+	+	+
Cœliac ... . .	+	0	0
External iliac .. . . .	+	+	+
Sacral .....	+	...	+
Internal iliac .. . . .	+	..	+
Common iliac.....	+	+	+
Lumbar .....	+		

### THE DUCTLESS GLANDS.

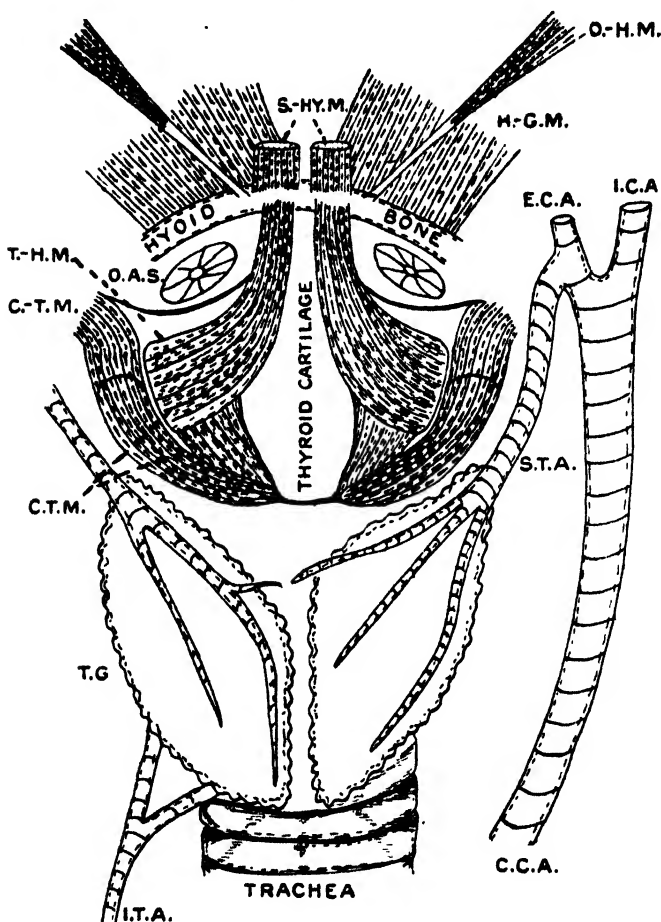
The *thyroid gland* (text-fig. 21, T.G.) consists of two thin unconnected lateral lobes lying against the sides of the lower end of the larynx and upper seven tracheal rings. Each lobe is triangular with the base upwards. It receives its blood-supply from the superior thyroid artery (S.T.A.) and its inferior thyroid branch on the left side, whereas the inferior thyroid artery (I.T.A.) on the right side is a branch of the subclavian artery. The arrangement of the arteries differs from that in the Chimpanzee. As regards the glands in the other Simiidae, there are records of separate or connected lobes in the Gorilla, and I have observed them connected in two Chimpanzees but separate in a third animal.

The *thymus gland* (text-fig. 22) is very large in this young animal. It extends from the lower third of the neck above to the level of the fifth costal cartilage, where it is almost in contact with the diaphragm. In the thorax there is a large left and a small right lobe in contact. In the upper part of the thorax and lower part of the neck these parts are fused and the gland is more finely lobulated. The thymus and lungs conceal the whole of the pericardium, except for a very narrow strip along the diaphragm.



The *spleen* is an elongated organ with a spindle-shaped outline. It is 4·3 inches long, 1·5 inches broad at its widest part, and

Text-figure 21.

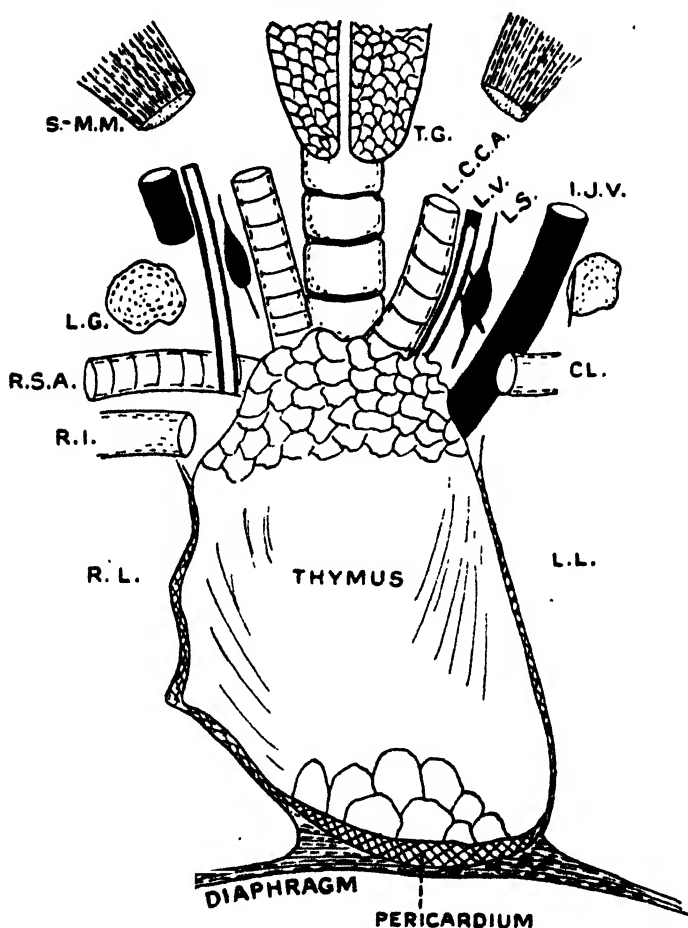


The thyroid gland and its relations. C.C.A., E.C.A., and I.C.A., common, external, and internal carotid arteries; C-T.M., crico-thyroid muscle; O-H.M. and S-HY.M., omo-hyoid and sterno-hyoid muscles thrown up: T-H.M., thyro-hyoid muscle; O.A.S., opening of air-vac. Other letters in text.

·3 inch thick. It is totally devoid of lateral fissures, and the hilum is long. It is very closely applied to the stomach. No

accessory spleens are present. The capsule is moderately thick. On section the structure appears sponge-like, the trabeculæ being

Text-figure 22.



The thymus gland and its relations. CL., clavicle; I.J.V., internal jugular vein; L.C.C.A., left common carotid artery; L.G., lymph gland; L.L. and R.L., lungs; L.V. and L.S., left vagus and sympathetic; R.I., first rib; R.S.A., right subclavian artery; S-M.M., sterno-mastoid muscle; T.G., thyroid gland.

very obvious. White granules representing Malpighian bodies are not visible.

## THE UROGENITAL ORGANS.

*Kidneys*:—No lobulation occurs on the outer surface. The right kidney is lower than the left one. On section the cortex is seen to be very thick as in the other Simiidae; and the thickness is relatively greater than in the Chimpanzee. Four fused pyramids are present, but these do not end in a papilla. The pelvis is small and devoid of fat. The venous drainage of the right kidney is great. The *ureter* has the usual course. The *bladder* is long, narrow, and pyriform. No urachus is present, but lateral ligaments are well marked. In the median line in front the longitudinal muscle coat forms a ribbon-like band. When the bladder is opened in the empty state, the mucous membrane exhibits many very pronounced longitudinal rugæ converging on the neck of the bladder. The ureteral orifices are close together. Each is overhung by an arch of mucous membrane, which is prolonged downwards on its inner aspect by a ridge (text-fig. 23 A). No actual ureteric papillæ exist. The urethral orifice (U.O.) is some distance from the ureteral openings (Ur.O.). Distally the urethra opens on the anterior vaginal wall as in the other Apes.

*External Generative Organs* (Pl. III. fig. A):—The external genitalia are very prominent in this young animal, for there is a great excess of subcutaneous fat. The mons veneris has many hairs. The clitoris (CL.) is well exposed; it has a well-marked, hood-like prepuce (PRE.) and a deep ventral groove. The labia majora are small. The vagina is very narrow and devoid of a hymen. In the Chimpanzee (72) the clitoris is cylindrical, and the prepuce is not so well marked. The vaginal orifice is very close to the under surface of the clitoris, so the vestibule is negligible in size. Perhaps it is better marked in the adult animal.

The *ovaries* (text-fig. 23 B) are large in this small animal. Each is 2 cm. long and .8 cm. broad. They lie with their long axes almost vertical; and each is surmounted by a cluster of fimbriæ. The greater part of each ovary lies above the level of the pelvic brim. The Fallopian tube (F.T.) ascends almost vertically on the front of the ovary, and the ovarian ligament (O.L.) descends towards the utero-tubal junction. No hydatid of Morgagni was seen on either ovary. No scars were observed on the surface of either ovary, as would be expected from the age of the animal. MacLead (48) has dealt with the Anthropoid ovary.

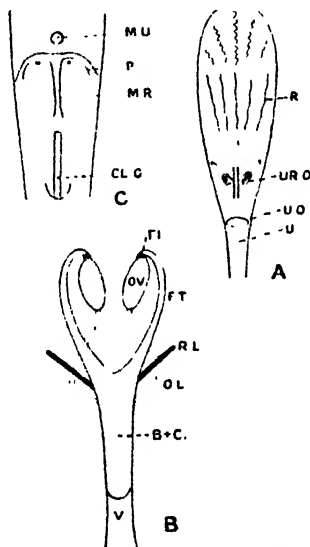
The *Fallopian tubes* (text-fig. 23 B) ascend in a comparatively straight line from the uterus to the upper poles of the ovaries; so the uterus at first sight appears bicornuate. The calibre of the tube remains practically uniform throughout. The fimbriæ (FL.) form a prominent cluster, and the ovarian fimbria is well marked.

At the angle between the tube and the uterus the round ligament (R.L.) is attached in the usual way. Between the tube

and the round ligament there is a cluster of tortuous, small arteries; and a few can be traced into the central extremity of the ligament.

The *Uterus* (text-fig. 23 B):—The uterus is long and narrow, and has no definite fundus. The Fallopian tubes diverge from it, and the angle between the tubes is acute. The body and cervix together form a long, thin-walled tube 1.1 inches long. And no distinction between body and cervix can be made out in this very young animal. The uterine mucosa is devoid of rugæ of any kind. No record of a bicornuate uterus in the Orang exists elsewhere.

Text-figure 23.



The bladder (A) and genital organs (B and C). C shows the anterior vaginal wall.

CL.G., groove on ventral surface of clitoris; B+C, body and cervix uteri; F.I., fimbria; M.R., median ridge; M.U., meatus urinarius; OV., ovary; P., pockets; R., rugæ; U., urethra; V., vagina. Other letters in text.

The *vagina* is a long cylindrical tube. The posterior wall is quite smooth. The anterior wall has two large pits separated by a strong septum. And the urethra opens into the vagina in front of them. In the distal part lies the beginning of the groove on the under surface of the clitoris (text-fig. 23 C).

The ovarian ligament (O.L.) runs to be attached to the middle of the side of the body of the uterus.

I have referred to many points in the anatomy of the male organs in another paper\*.

The fœtus has been described by Trinchese (77).

\* P. Z. S. 1923, pp. 1001-1006.

## THE ORGANS OF RESPIRATION AND VOICE.

*Air-sinuses in Skull*:—In the adult Orang the sphenoidal and maxillary sinuses are present, but the former are smaller than in the Chimpanzee. Frontal sinuses are absent, their place being taken by cancellous bone. In this very young animal no sinuses have as yet formed, but the sphenoid and maxillæ are entirely composed of cancellous tissue (Pl. III. fig. B).

*Nasal Fossæ* (Pl. III.):—Two turbinate bones are present on each side. The inferior turbinate bone (I.T.B.) is long and entire, whereas it is bifid in the Chimpanzee; it is not very inflated. The middle turbinate bone (M.T.B.) is large and expanded. No superior turbinate bone exists. No bulla ethmoidalis is present. The nasal vestibule is small, and its mucosa has not many glandular orifices. The septum nasi is membranous and cartilaginous, for no ossification has taken place in its component elements.

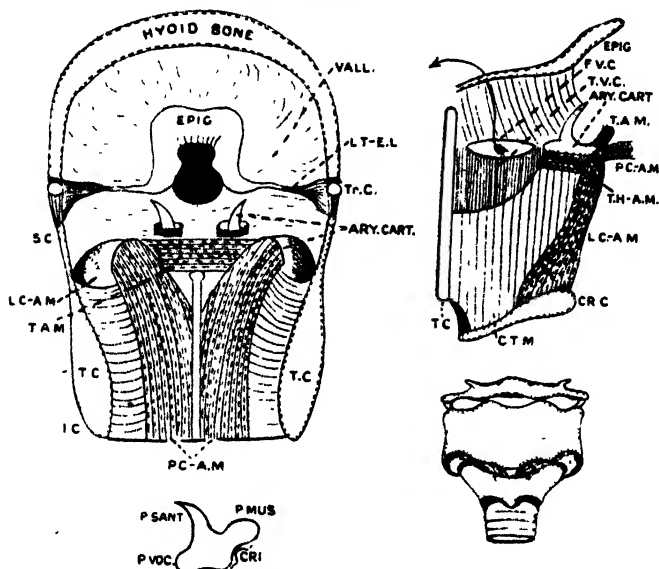
*Larynx* (text-fig. 24):—The larynx has been described by Duvernoy (24), Giacomini (29), and Koerner (45). It differs in many ways from that in the Chimpanzee and Man. It is connected as usual to the tongue, and the vallecule (VALL.) are shallow.

The *thyroid cartilage* (T.C.) is broad, and its vertical height is small. It has shallow median notches above and below; in the Chimpanzee (72) both notches are deep, and in Man there is only the superior notch. Laterally it suddenly passes into the cornua. The superior cornu (S.C.) is connected to the hyoid bone by a ligament, in which there is a small triticeal cartilage (Tr.C.). The massive inferior cornu (I.C.) is connected to the cricoid cartilage by a ligament. The *epiglottis* (EPIC.) is folded on itself in such a way that the superior border and laryngeal aperture look backwards. It is prolonged laterally by cornua, which are connected by lateral thyro-epiglottic ligaments (L.T.E.L.) to the thyro-hyoid joints. The *cricoid cartilage* (CR.C.) is broad and thick, with a median dorsal ridge. The anterior part is composed of two bow-shaped pieces of cartilage, which unite in front to form a triangular plate. The apex of the plate is connected to the front of the trachea by a small, strong ligament. No *cartilages of Wrisberg* were seen. The *cartilages of Santorini* have not been separated from the arytenoid cartilages. The *arytenoid cartilages* (ARY.CART.) are large and have three well-marked processes (text-fig. 24). The muscular process (P.MUS.) is large and receives four muscles—lateral crico-arytenoid, posterior crico-arytenoid, thyro-arytenoid, and arytenoideus. The vocal process is not so large. The process of Santorini (P.SANT.) is long, sharp, and passes upwards through a sheath of mucous membrane. The muscular process is above the crico-arytenoid articular facet. The *processus vocalis* (P.VOC.) is globular.

The *thyro-hyoid muscles* and their relations to the orifices of

the air-sacs have already been figured (text-fig. 21) and described. The *crico-thyroid muscle* (text-fig. 21) consists of the same parts as in Man. The *posterior crico-arytenoid muscle* (text-fig. 24, P.C-A.M.) runs from the back of the cricoid cartilage and the side of the median crest to the processus muscularis of the arytenoid cartilage. The two muscles are fused below. The *arytenoideus transversus* (T.A.M.) connects the two arytenoid cartilages, but there is no trace of the *arytenoideus obliquus*. In the Chimpanzee and Man both oblique and transverse muscles exist. The *lateral crico-arytenoid muscle* (L.C-A.M.) runs from the upper border of the bow-shaped anterior cricoid lumina to the front of the processus muscularis of the arytenoid

Text-figure 24.



The larynx. The arrow passes into the air-sac. Letters in text.

cartilage. The *thyro-arytenoid muscle* (T.H-A.M.) which is broad, thin, and indivisible, runs from the back of the anterior part of the thyroid cartilage to the outer border and processus muscularis of the arytenoid cartilage. Some deep fibres get into the outer side of the true vocal cord.

The *thyro-hyoid membrane* is thicker in the centre than at the sides, where it is pierced by the air-sacs where they communicate with the laryngeal ventricles. The *crico-thyroid membrane* (C-T.M.) has a strong central part, or conus elasticus, which is firmly united to the opposing borders of the thyroid and cricoid cartilages. The lateral parts of the membrane are thin; they

are prolonged upwards to become continuous with the true vocal cords. The *ary-epiglottic folds* are weak.

*Vocal Cords*:—The false cords (F.V.C.) do not project into the larynx. The true cords (T.V.C.) are very thin and hardly project inwards. Between the cords lie the elliptical openings of the ventricles. The latter are small and lead upwards and forwards into the air-sacs. In the back of the true cords the well-marked *processus vocalis* of the arytenoid cartilage on each side is easily felt.

*Laryngeal Joints*:—The thyro-hyoid ligaments, which connect the hyoid bone and superior thyroid cornua, contain triticeal cartilages (Tr.C.). The inferior thyroid cornua are connected to the flat surface of the anterior cricoid lamina by a strong ligament. No actual articular facets lie on the parts of these cartilages which are connected in the joint. The crico-arytenoid joints have strong capsules, particularly posteriorly, but I could not detect a definite check ligament similar to that in Man. The slightly concave surface of the arytenoid cartilage is not closely moulded over the more strongly-marked convex and elongated articular surface of the cricoid cartilage.

The *tracheal cartilages* are defective behind.

The *lungs* are entire, and all authors who have hitherto examined them, except Fick (26), observed the same condition. On looking at the hilus, it is seen that the structures entering and leaving the lungs are arranged as in Man. An undivided state of the lungs also occurs in *Phascolarctos*, *Bradypus*, and some Cetacea.

The air-sacs have been fully described by many authors, Milne-Edwards (50) and Duvernoy (24) giving most particulars. I have nothing to add to their accounts.

#### THE NERVOUS SYSTEM\*.

The olfactory, trochlear, and abducent nerves show nothing peculiar.

The *optic nerve* is long and thick. The *arteria retinae centralis* enters its inner side, and it is surrounded by numerous ciliary arteries and nerves. The intra-orbital measurements are given with the eye (see p. 437).

The *oculomotor nerve* is as in Man, except that the motor root of the ciliary ganglion comes from the inferior division of the nerve itself and not from the nerve to the inferior oblique muscle. No twig runs from the superior division to the ciliary ganglion as in the Chimpanzee (72).

The *trigeminal nerve* differs in several ways from that in Man. The Gasserian ganglion is large. It is placed on the petrous part of the temporal bone where it forms the back wall of the middle cranial fossa, and it reaches close to the floor of the fossa.

\* The brain had been torn up by the ruptured cerebral artery and injection material, so it was not examined.

It is thus lower down than in Man. Three divisions radiate as usual from the ganglion. The *ophthalmic division* divides into lachrymal, frontal, and nasal branches, but these have nothing peculiar about them. The *maxillary division* is long and thick. It passes through the middle cranial fossa, sphenomaxillary fossa, and infra-orbital canal; and it ends on the face as the infra-orbital plexus. In this young animal the infra-orbital groove is a mere linear slit, so the nerve does not gain the orbit at all. In text-fig. 13 the comparison between the orbital floor and back wall in Man, the adult Orang, and this young animal are shown. Should the conditions in this young animal be typical, it would seem that the formation of an infra-orbital groove is a post-natal change. The nerve gives off the following branches:—

a; several small *meningeal twigs*.

b; two *spheno-palatine nerves* to Meckel's ganglion. The latter gives off palatine, nasal, and nasopalatine nerves, which course generally as in Man.

c; *posterior dental nerve*, which supplies the back molar teeth and gums.

d; *orbital branch*. This enters the orbit and passes forwards on its lateral wall. It breaks up into several branches. Temporal and malar nerves pass through foramina in the malar bone to the skin of the face. Other branches pass forwards, communicate with the lachrymal nerve, and supply the gland, conjunctiva, and skin.

e; *infra-orbital nerve*. This nerve, which continues the maxillary nerve, gives off middle and anterior dental nerves to the teeth as in Man. It appears on the face as the infra-orbital plexus, which supplies the skin of the lower eyelid, cheek, lip, and nose. Branches also go to the mucosa of the upper lip.

The *mandibular division of the trigeminal* has the same course and divisions as in Man and the Chimpanzee. Its lingual branch is joined by the chorda tympani as usual. The buccal branch forms a rich plexus. The mylo-hyoid branch runs in a groove, which is more posterior than in Man in the adult animal. In this very young animal there is no trace of a groove. A small groove also runs upwards and forwards towards the last molar tooth in the adult animal from the middle of the rudimentary lingula. In Man this groove is faintly marked, and its course and termination are different.

*Ganglia connected with the Trigeminal Nerve*:—The ciliary ganglion is small and spherical, and lies close to the eyeball in the interval between the optic nerve and external rectus muscle. It has the same connections as in Man. Meckel's ganglion may be present as a separate body, or it may be fused with the maxillary nerve. The otic ganglion was not definitely detected.

The *sixth nerve* is not peculiar.

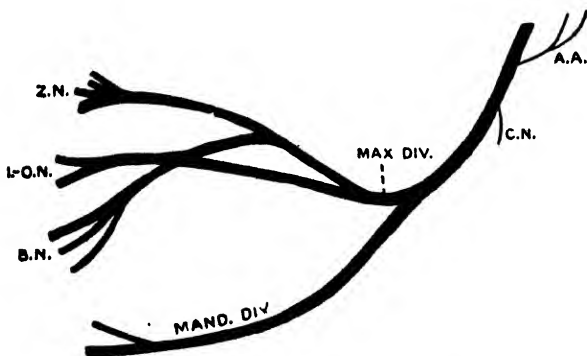
The *facial nerve* (text-fig. 25) differs from that in Man and the Chimpanzee (72); and the conditions in this animal differ from



those figured by Ruge (62). After emerging from the stylo-mastoid foramen, the nerve has a long course before it divides into its two terminal divisions. The trunk gives off auricular (A.A.) and cervical (C.N.) nerves. Of the two terminal divisions the upper or *maxillary nerve* (MAX.Div.) is the larger. The maxillary nerve does not give off temporal branches. It divides into zygomatic (Z.N.) and infra-orbital (I-O.N.) branches. The former supplies the orbicularis oculi and zygomatic mass; and the latter supplies the orbicularis oculi and muscles of the upper lip. The infra-orbital nerve also gives off the buccinator nerve (B.N.) to the buccinator muscle. The *mandibular division of the facial nerve* (MAND.Div.) is distributed to the muscles of the lower lip.

These branches end in exceedingly rich nerve plexuses, but they are not so intricate in this animal as in the illustration by Ruge (62). Moreover, he shows a more complicated mandibular series of nerves. The branches of the facial nerve intermingle with the

Text-figure 25.



The maxillary division of the trigeminal nerve. Letters in text.

zygomatic, infra-orbital, buccal, and mandibular branches of the trigeminal nerve. The *chorda tympani* is as in the Chimpanzee and Man.

The *auditory nerve* was not traced.

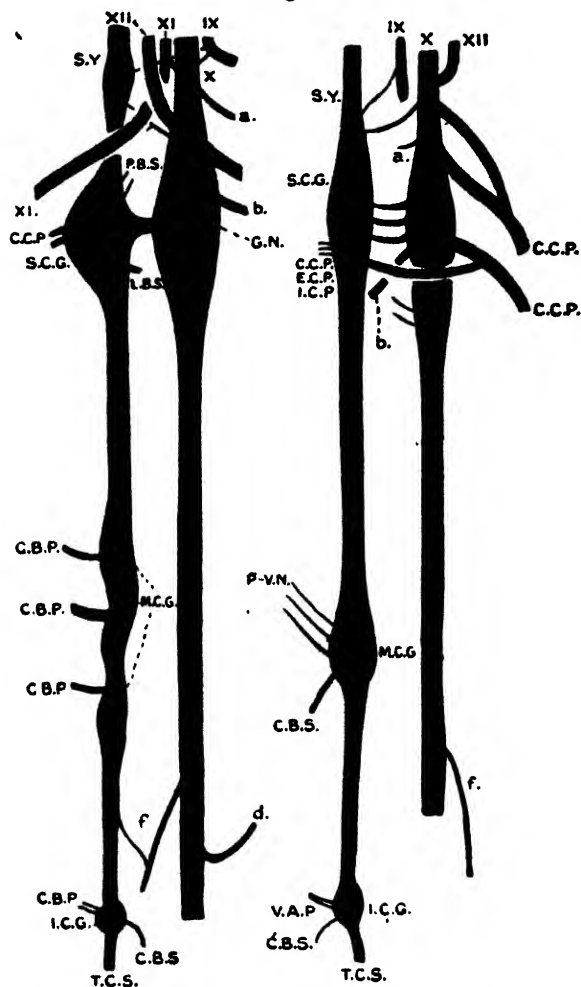
The *glossopharyngeal nerve* has the same course and distribution as in Man.

The *vagus nerves* (text-figs. 26 & 27) run separately from the sympathetic nerves on both sides of the neck, whereas there was a vago-sympathetic cord on the right side in three Chimpanzees examined by myself. Within the jugular foramen the vagus is closely applied to the ninth and eleventh nerves, and it is strongly fused with the hypoglossal nerve below the base of the skull. The ganglion nodosum is well marked on each side.

Within the thorax each vagus breaks up into a posterior pulmonary plexus. The left vagus is not reconstituted again

from the plexus; some filaments run through the oesophageal opening in the diaphragm, and others wind round the oesophagus to join the right vagus nerve. Two cords emerge from the right posterior pulmonary plexus; one, a thick cord, receives filaments

Text-figure 26.



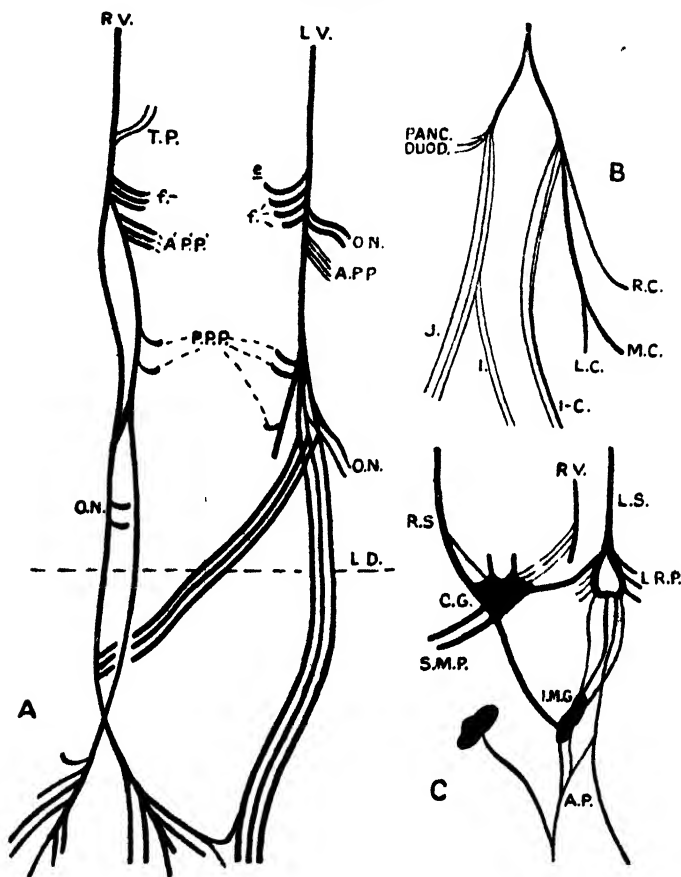
The cervical parts of the vagus and sympathetic nerves. Letters in text.

from the left vagus, and the other, a thin cord, joins the thick one in the abdomen.

Within the abdomen (text-fig. 27 A & B) the left vagal filaments supply the anterior wall of the stomach, and some run

along the lesser curvature to the pylorus. The right vagus supplies the two walls of the stomach along the lesser curvature, but the main mass passes on behind the coronary and splenic

Text-figure 27.



The thoracic and abdominal parts of the vagus and sympathetic nerves. A.P., aortic plexus; C.G., coeliac ganglia; DUOD., duodenal nerves; I., ileal nerves; I-C., L.C., M.C., R.C., ileo-colic, left colic, mid colic, and right colic nerves; I.M.G., inferior mesenteric ganglion; L.D., line of diaphragm; L.S. and R.S., splanchnic nerves; L.R.P., left renal plexus; L.V. and R.V., vagus nerves; PANC., pancreatic nerves; S.M.P., superior mesenteric plexus. Other letters in text.

arteries to the side of the superior mesenteric artery at its origin. At that point it communicates with the coeliac and superior mesenteric plexuses (text-fig. 27 C); and branches run along the

ileo-colic artery to the cæcum. Branches can also be traced along the left and middle colic arteries, thus supplying the large intestine as far down as the splenic flexure of the colon; but it may be that the branches to the colon are really composed of sympathetic filaments, which have entered the vagus high up.

The branches of the vagus nerves are as follows:—

A. *Cervical Branches* (text-fig. 26).

1. Communicating to the glosso-pharyngeal nerve (IX).
2.       "       "       accessory nerve (XI).
3.       "       "       sympathetic cord (S.C.).
4.       "       "       superior sympathetic ganglion (S.C.G.).
5. Pharyngeal nerve (*a*) to pharyngeal plexus.
6. Superior laryngeal nerve (*b*).
7. Cardiac nerve (*f*).
8. Right recurrent laryngeal nerve (*d*).

B. *Thoracic Branches* (text-fig. 27 A).

1. Left recurrent laryngeal nerve (*e*).
2. Three left and three right cardiac nerves (*f.f.*).
3. Anterior pulmonary plexuses (A.P.P. and A'.P'.P').
4. Posterior pulmonary plexuses (P.P.P. and P.P'.P').
5. Oesophageal nerves (O.N.).
6. Tracheal branches of right vagus (T.P.).

The *accessory* and *hypoglossal* nerves are both much as in Man.

*Nerves of the Arm.*

*Brachial Plexus* (text-fig. 28):—In this animal the plexus is formed by the anterior primary divisions of the lower four cervical and first dorsal nerves. And communicating filaments link it to the fourth cervical and second dorsal nerves as in Man.

The fifth and sixth cervical nerves each divide into anterior and posterior divisions. The anterior divisions unite and the posterior divisions unite, so there is no upper trunk formed by the fifth and sixth nerves as there is in Man. In one Chimpanzee there was no upper trunk (72), but in another animal there was a trunk as in Man. The seventh cervical nerve forms a middle trunk, which divides later into anterior and posterior divisions. The eighth cervical and first dorsal nerves form a lower trunk which likewise divides.

The anterior divisions of C5 and C6 unite to form a cord, which gives off part of the outer head of the median nerve and is continued as the musculo-cutaneous nerve. The anterior division of C7 unites with part of the latter to complete the outer head of the median nerve (O.H.M.). And the anterior division of the lower trunk forms the inner head of the median nerve (I.H.M.), the ulnar and internal cutaneous nerves; it communicates with the anterior division of C7. The posterior divisions of all the

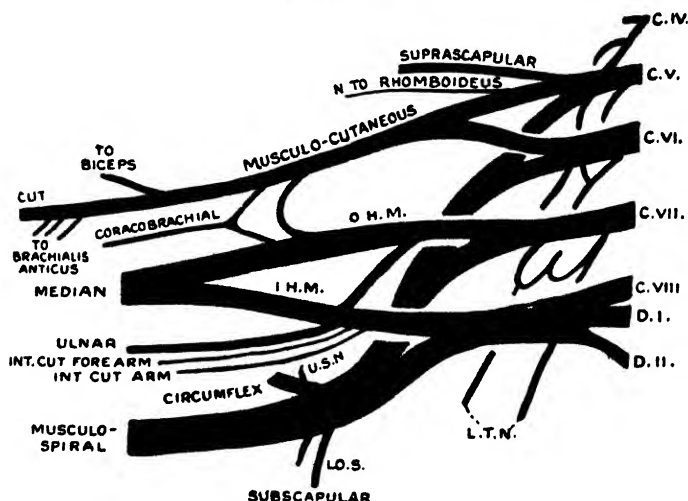
nerves entering into the plexus unite to form the thick posterior cord.

The *suprascapular nerve* arises from the anterior division of C 5. Accompanied by the suprascapular artery it passes over the base of the scapula, but there is no notch on the bone at the point of crossing as in Man. Its course and distribution are as in the other Apes and Man.

The *nerve to the rhomboid muscles* also comes from C 5.

The *musculo-cutaneous nerve* runs downwards and, after giving off the nerve which unites with a filament of the median nerve to form the nerve to the coraco-brachialis, it passes between the two parts of that muscle and sends off a thick nerve to the biceps; that nerve divides into a branch for each belly of the biceps. In

Text-figure 28.



The brachial plexus. Letters in text.

the lower part of the arm it gives three twigs to the brachialis anticus, passes under the biceps, and enters the forearm as a cutaneous nerve (Cut.), which can be traced to the radial side of the wrist.

The *median nerve* gives off a branch which unites with a branch of the musculo-cutaneous nerve to form the nerve to the coraco-brachialis. No other branches are given off in the arm. As it runs down it lies entirely behind the brachial artery, a position which it also occupies in the other Apes. On the right side it passes between the two bellies of the pronator radii teres as a broad band; on the left side it passes as the nerve and several branches. Branches in the upper part of the forearm enter the pronator radii teres, flexor carpi radialis, flexor sublimis digitorum,

*palmaris longus*, *flexor profundus digitorum*. It does not communicate with the ulnar nerve. At the wrist it passes deep to the carpal arch (anterior annular ligament) and divides into two branches. The first, or lateral branch, supplies the thenar muscles and gives cutaneous branches to both sides of the thumb. The second, or medial branch, divides to supply the adjacent sides of the first, second, and third fingers, and it sends a branch to the first two lumbrical muscles. The median nerve also gives off an anterior interosseous nerve, which supplies the *flexor profundus digitorum* and *pronator quadratus*. Hepburn (35) also shows how the *flexor profundus* may be supplied by both median and anterior interosseous nerves. He also mentions that the ulnar and median nerves communicate in the Chimpanzee, Gorilla, and Gibbon. The Gorilla, Chimpanzee, and Man have a similar cutaneous distribution to that in the Orang, but the median nerve also supplies the third lumbrical muscle in the Chimpanzee. In the Gibbon the anterior interosseous nerve does not supply the *pronator quadratus*.

The *Musculo-Spiral Nerve* has the same course as in the Chimpanzee and Man. It ends by dividing into the radial and posterior interosseous nerves proximal to the external condyle of the humerus. In the arm it supplies the skin and the triceps, *extensor carpi radialis longior*, *supinator longus*, and *dorso-epitrochlearis*. It does not supply the *brachialis anticus*, and Hepburn (35) points out that the Gorilla is the only Ape in which this muscle is innervated by the musculo-spiral nerve. The radial nerve (superficial division) runs down on the deep surface of the *supinator longus*, winds round the wrist, and supplies the skin of the outer one and a half digits. The posterior interosseous nerve (deep division) passes through the *supinator brevis* to the back of the forearm, where it supplies the same muscles as in Man. The filament which runs to the wrist joint in the Chimpanzee is also present in the Orang. And it supplies the skin of the dorsum of the hand and digits.

The *Ulnar Nerve* from the inner cord of the plexus is large. Its general course is as in the Chimpanzee and Man. It gives off no branches in the arm. In the forearm, just at the level of the elbow joint, it gives off an articular twig. It enters the forearm between the two origins of the *flexor carpi ulnaris*. At the head of the ulna it divides into two. One branch supplies the skin of the wrist, and the palmar and dorsal aspects of the hand in the region of the little finger. The second branch divides into two; one half supplies the *hypothener* muscles, and the skin of the inner side of the little finger and the adjacent sides of the little and ring fingers; the other half passes into the hand deep to the *flexor tendons*, and divides into branches for the *interossei*, *adductor obliquus pollicis*, *adductor transversus pollicis*, and the two inner lumbrical muscles. Hepburn (35) states that it also sends a branch to the deep head of the *flexor brevis pollicis*. The cutaneous distribution is similar

in the Gorilla, Chimpanzee, and Orang, but, as shown in Hepburn's account, its muscular supply differs, particularly in the supply to the lumbricales and contrahentes.

The *circumflex nerve* runs and ends as in the Chimpanzee and Man. It gives off the upper subscapular nerve (U.S.N.). The *long subscapular* for the latissimus dorsi and the *lower subscapular* (Lo.S.) for the teres major and subscapularis come from the posterior cord of the plexus. The *internal cutaneous nerves* show nothing different from the conditions in the Chimpanzee and Man.

The *long thoracic nerve* (L.T.N.) is very interesting. It is divided into two parts. One part, from C 4, C 5, and C 6, is slender, and runs to the upper part of the serratus magnus. The other part, from C 7, is stout, and runs to the rest of the muscle. It communicates with the other part. The first part is accompanied by a branch of the vertebral artery (text-fig. 15 B), and the second part is accompanied by the true long thoracic artery. The nerves to the upper part of the serratus magnus in the Chimpanzee are also of great interest (72).

The *intercosto-humeral nerve* courses as in Man. It does not communicate in this animal with the internal cutaneous nerve of the arm and with the lateral branches of the first and third intercostal nerves as I observed it doing in one Chimpanzee out of three examined (text-fig. 9).

The *phrenic nerve*, from C 3, C 4, and C 5, courses as usual in the Mammals. A short distance proximal to the diaphragm it divides into two equal branches, which diverge and pass through the diaphragm to the under surface; and branches of each half do likewise. No *arteria comes nervi phrenici* is present. And I did not observe any communication with the sympathetic as Eisler (25) and Duckworth (20) record in the Gorilla in the neck. No communication was found by me in three Chimpanzees. In the abdomen it communicates with phrenic branches of the sympathetic.

#### *The Lumbar Plexus* (text-fig. 29).

The four lumbar nerves enter into the formation of the plexus. Loops unite the nerves, but I was unable to detect a loop connecting the last dorsal and first lumbar nerves. The fourth lumbar nerve receives a communication from the third lumbar nerve and forms the thick lumbo-sacral cord. The plexus has been described by Bolk (8), Ihering (40), Westling (84), and others.

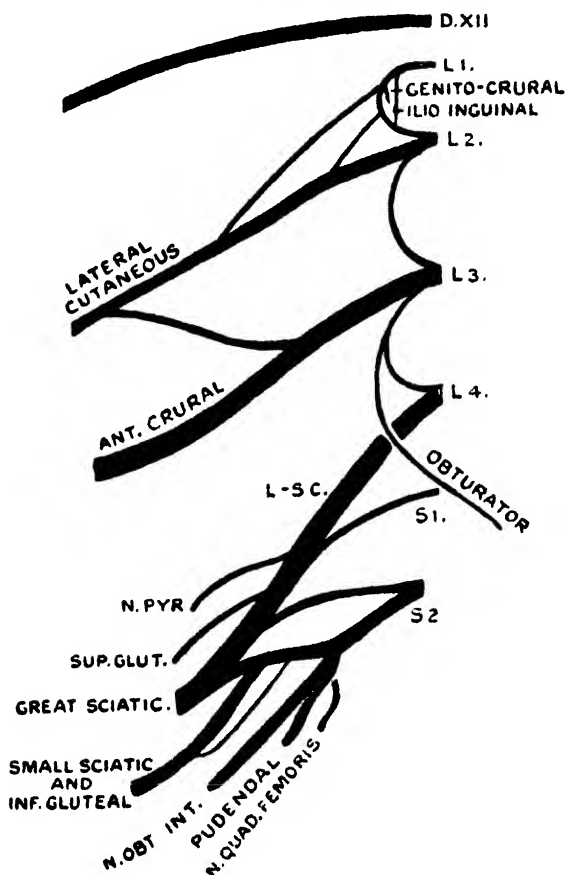
The *genito-crural* and *ilio-inguinal* nerves arise from the first lumbar nerve. Hepburn (35) gives a similar origin.

The *lateral cutaneous nerve of the thigh* arises differently on the two sides. On the left side it springs from the first and second lumbar nerves. On the right side it is formed from upper and lower parts; the former is composed of twigs coming from L1 and

L2, and the latter is a thick nerve springing from the anterior crural nerve. The distribution of the nerve is over the anterior and lateral aspects of the thigh.

The *anterior crural nerve* arises from L 1, L 2, and L 3. It gives off two branches to the iliacus and one branch to the psoas magnus within the pelvis. In the thigh it gives off middle and

Text-figure 29.



The lumbo-sacral plexus. Letters in text.

internal cutaneous nerves, and the long saphenous nerve which ends in the skin of the inner side of the foot and hallux. Muscular branches are also given off to the pectineus, sartorius, and component parts of the quadriceps extensor. The saphenous nerve is the apparent continuation of the parent nerve.

The *obturator nerve* arises, according to Hepburn (35), from



L 1 and L 2. In my specimen it arises from L 2 and L 3. It has the usual course, and ends in the same muscles as in Man and the Chimpanzee.

The *pudendal nerve* arises from S 2 along with the nerve to the obturator internus and nerve to the quadratus femoris. The *nerve to the pyriformis* springs from the lumbo-sacral cord above, and the *superior gluteal nerve* arises below the point where the cord receives the first sacral nerve. The small sciatic and inferior gluteal nerves come from S 2, and form a plexus in the buttock.

The *Great Sciatic Nerve* is formed by the lumbo-sacral cord (L.S.N.) and first and second sacral nerves. It has the usual course, and ends at the junction of the middle and lower thirds of the thigh by dividing into external and internal popliteal nerves. Possibly the level of the bifurcation varies individually as in Man. At the upper part of its extra-pelvic course it gives off a well-marked nerve to the hamstring muscles. At the lower part of its course the part of the nerve which will become the internal popliteal nerve gives off two filaments to the femoral or short head of the biceps. The great sciatic nerve also supplies the ischial head of the adductor magnus.

The *Internal Popliteal Nerve* is the larger of the two terminal divisions of the great sciatic nerve. Hepburn (35) points out that it is really composed of the filaments of the sacral nerves, which enter into the great sciatic nerve. It supplies the gastrocnemius, soleus, and popliteus, and gives off the *external saphenous nerve*. The latter supplies the skin of the outer side of the foot and little toe. Hepburn states that the external saphenous and musculo-cutaneous nerves communicate, but the communication must have been broken in my animal in the process of skinning.

The *Posterior Tibial Nerve* is the continuation of the internal popliteal nerve at the lower border of the popliteus muscle. As it courses down the thigh, it gives branches to the deep flexor muscles, the skin of the heel, and the abductor minimi digiti. A well-marked nerve of communication runs between it and the external saphenous nerve. It ends by dividing into external and internal plantar nerves. No nerve runs to the soleus as in Man, and there are no branches to the anterior tibial muscles and peronei as in a Chimpanzee examined by me (72). The branch to the anterior tibial muscles in that animal must have consisted of filaments which should have passed higher up from the great sciatic nerve to the external popliteal nerve.

The *Internal Plantar Nerve* soon divides into two nerves of equal size. The inner division soon gives off a branch which accompanies the hallucial branch of the internal plantar artery and supplies the skin on the outer side of the hallux, the abductor hallucis, adductor hallucis, and flexor brevis hallucis. After giving off the hallucial nerve the inner division ends as the cutaneous nerve of the inner side of the second digit.

The *anterior tibial nerve* gives branches to the *tibialis anticus*, *extensor longus hallucis*, and *extensor longus digitorum*. It does not reach the foot. Hepburn (35) observed the same arrangement.

The *musculo-cutaneous nerve* supplies the peroneal muscles and the skin of the dorsum of the foot except the borders of the sole, the inner side of the hallux, and the outer side of the fifth digit. The cutaneous supply is a little greater in the Chimpanzee (72).

*The Sympathetic Nervous System* (text-figs. 26 & 27).

The number of internal carotid nerves on each side is one, whereas there are several in the Chimpanzee (72). The left superior cervical ganglion (S.C.G.) is long and fusiform, but the right one is flat and irregular. Middle cervical ganglia (M.C.G.) are both well marked, but the inferior cervical ganglia (I.C.G.) are small. The following are the cervical branches (text-fig. 26):—

A. *From the superior ganglion and nerves above:*

1. Communicating to the glossopharyngeal (c. IX), vagus (c. X), hypoglossal (c. XII), and cervical plexus (C.C.P.).
2. Pharyngeal (P.B.S.) and laryngeal (L.B.S.) nerves.
3. Carotid plexus (C.C.P., E.C.P., I.C.P.).

B. *From the middle cervical ganglion:*

1. Communicating to the brachial plexus (C.B.P.).
2. Prevertebral branches (P-V.N.).
3. Cardiac nerve (C.B.S.).

C. *From the inferior cervical ganglion:*

1. Communications to the brachial plexus (C.B.P.).
2. Vertebral arterial plexus (V.A.P.).
3. Twigs to the annulus of Vieussens (A.V.).
4. Cardiac nerve (C.B.S.).
5. Thoracic gangliated cord (T.C.S.).

The right recurrent nerve has the same course as in the Chimpanzee and Man. It communicates with the sympathetic.

The thoracic cords have fewer ganglia than the number of intercostal nerves, so that rami communicantes appear as branches of the cord. The trunks form the splanchnic nerves, the left one entering the left renal plexus, and the right one passing into the solar plexus (text-fig. 27 C).

### THE EYE AND ITS APPENDAGES.

The eyes are prominent and close together, but Fick (26) points out that the interpupillary distance is not much less than in Man. There are no marked eyebrows. The lids have

thickened margins, and the upper one has numerous black eyelashes. The lachrymal papillæ are practically non-existent.

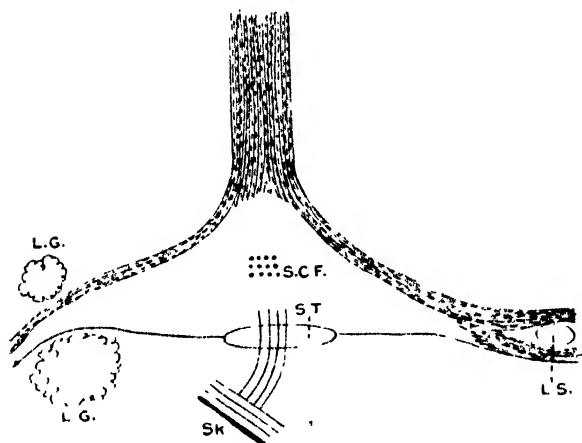
On the deep surface of the upper lid there are no visible ridges produced by Meibomian glands. The palpebral conjunctiva is not pigmented, but the bullar conjunctiva is bluish in colour. Milne Edwards (50) figures two Orangs with dead-white bullar conjunctivæ. In four Chimpanzees I observed variations in the pigmentation of the conjunctiva.

The lacus lachrymalis is a mere slit, and the plica semilunaris is small. It contains no cartilage.

The orbital roofs are dome-shaped. On opening the roof a dense capsule of Tenon is seen to envelop the orbital contents.

*Ocular Muscles*:—The *levator palpebræ superioris* arises in the usual way. Passing forwards it spreads out, and has a wide

Text-figure 30.



The levator palpebræ superioris. Letters in text.

fibro-muscular insertion. Some fibres pass forwards through the orbicularis oculi to the skin of the upper lid (text-fig. 30, Sk.). Others are attached to the upper border and anterior surface of the superior tarsus (S.T.); and others again pass to the superior conjunctival fornix (S.C.F.). A lateral band splits the lachrymal gland (L.G.: L.G.) and is attached to the deep surface of the malar bone. And a mesial band splits into two slips which embrace the lachrymal sac (L.S.) and are inserted into the lachrymal bone. There is some fusion between the levator and the superior rectus, and the branch of the third nerve to the levator pierces the rectus. The *superior rectus* has the usual origin and insertion. It receives a well-marked branch of the ophthalmic artery. The *superior oblique* is so closely apposed to the inner wall of the orbit that it does not appear on the upper surface of

the globe. It is cylindrical, and has the usual origin. The long, slender, strong tendon runs through a trochlea, and has the usual insertion. The tendon is connected by strong fascia to the superior rectus; and it does not expand towards the globe as in the Chimpanzee (72). The *external rectus* has great vertical depth. It has the usual two heads, but no structures pass between them as in Man. The *inferior oblique* remains fleshy throughout, whereas it ended in a tendon in a Chimpanzee examined by myself (72). It is attached obliquely to the posterior aspect of the globe, and this insertion enables the Orang to move its eyes considerably upwards and inwards without moving its head. The *internal rectus* is as in Man. The *inferior rectus* is a strong, cylindrical muscle with a more intimate attachment to the globe of the eye than the other muscles. No *retractor bulbi* exists. Otteley (51) describes many of the above conditions, and points out that the recti are attached more anteriorly than in Man.

The globe of the eye is small, and the optic nerve within the orbit is long and thick, as can be seen in the following table:—

Antero-posterior length of orbit .....	36 mm.
"    "    diameter of globe.....	14 "
Length of optic nerve .....	27 "
Diameter of "    "    .....	3 "

The muscle, vessels, and nerves are all long, for the globe lies far forwards. Much fat is present, and this probably accounts for the prominence of the eyes in this animal. In Man variations in the amount of fat modify the degree of protrusion of the globe.

The *lacrimal gland* consists of two parts separated by a process of the levator palpebræ superioris (text-fig. 30, L.G.) The *lacrimal sac* is embraced by fibres of the levator palpebræ, and is compressed by fibres from the orbicularis oculi. The sac and duct exhibit nothing peculiar.

Lindsay Johnson (41) pointed out that the ophthalmoscopic appearances in the eyes of the Gorilla, Chimpanzee, and Orang are like those in the negro, but they have clear fibres round the optic disc. He shows that these fibres are numerous in Man in the congenital defect known as opaque nerve fibres. In this animal the retina had disappeared by the time this stage in the dissection had been reached. The disc appeared much smaller than the area of the cross-section of the nerve.

No injection material had entered the arteria retinae centralis. The ciliary arteries pass into pits in the sclera round the optic nerve entrance.

The relations of the structures in the orbit differ in some ways from those in Man. No nerves and vessels pass between the heads of the rectus externus muscle; and the ophthalmic artery, which is shorter than in Man, always remains on the outer side of the optic nerve. Details are also given with the vessels and nerves in other parts of this paper.

*The Auditory Apparatus.*

Several observers have pointed out that the auricle is more degenerate than in other Apes; and Pocock (57) regards this as being associated with the retiring habits of the animal.

The auditory ossicles, like those in the Gorilla, resemble those in Man in a few points; but those in the Chimpanzee, taken as a whole, resemble those in Man most closely (72).

## THE HAIRS (Pl. IV. fig. B).

The following account of the hairs by Mr. J. Martin Duncan, F.R.M.S., should be contrasted with his account of the hairs in the Chimpanzee (72).

The microscopic appearance of the hair of the Orang presents a marked contrast to that of either the Chimpanzee or the Gorilla. This is due to the irregular outline of the strongly-marked, imbricate cuticular scales, with their crenulated edges. The colour of the hair being a fine tawny red, due to diffuse pigment, the dark wavy outline of the cuticular scales stands out in strong relief, producing a most striking and characteristic picture, making the hair quite distinctive from that of any other Anthropoid.

The dense medulla is of the continuous, homogeneous type.

The cutaneous pigmentation in the Apes has been described by Adachi (1), and the flexure lines and papillary ridges by Duckworth (20), Schlaginhaufen (64), and Wood Jones (85).

I desire to express my thanks to Miss Kahan and Messrs. Aurounin, Meneces, Ogden, and Scheinfein, students in the Anatomy Department of University College, for their assistance in the dissection. I desire also to thank Mr. R. H. Burne for the loan of an interesting skull.

## COMPARATIVE PHYSIOLOGY.

The Orang differs in its habits and demeanour from the other Apes. It does not possess the grace and agility of the Gibbons, the ferocity of the Gorilla, or the intelligence of the Chimpanzee. It is a heavy, sluggish animal; and, like other sluggish animals, such as the Sloth, it is very tenacious of life.

Travellers have stated that the Orang carefully tests the branches before it moves, even when it is pursued; but its sheer weight, which may amount to eleven or more stone, sometimes breaks them. The animal then falls to the ground, and bones are frequently broken. Duckworth (21) points out that the Orang is more liable to fracture than all other Apes, and he shows photographs of injured bones. Next in frequency comes the Gorilla, which is liable to fractures of the large sagittal crest. As the Gorilla is the most terrestrial Ape, it is probable

that the fractures are due to causes such as fighting and the fall of large branches of trees. The healing of the fractures may or may not be accompanied by excessive callus formation. From a study of Duckworth's photographs we may assume that the animals were in some cases rendered helpless, and they must have been fed by companions. Wallace (80, 81) describes cases of fractures of great or medium severity in young and adult animals.

The Apes resist shock very well. Possibly they have very resistant vaso-motor centres and reflexes, or their nervous system as a whole is not so delicately tuned up as in Man. Duckworth mentions a specimen in which the jaws were smashed and the facial skeleton was separated from the base of the skull. In spite of the shock and cerebral concussion which must have accompanied such a severe injury, the animal lived till signs of repair of the bones were clearly manifested. Man can tolerate very severe injuries, but very few recover from fractures of the base of the skull.

The Gorilla has been obtained at altitudes of 10,000 feet above sea-level, and it is probable that severe circulatory and other changes would occur if it were brought down alive to sea-level. Aggazotti \* has described the effects of alterations in barometric pressure on the Orang, but I have not been able to obtain his papers.

The young Orang, like the young Chimpanzee and Gibbon, is timid, and one of the manifestations of fright is a disturbance in the balance of the ocular muscles. In one animal I observed the left eye turned upwards and inwards, whilst the right eye was turned downwards and inwards. Squinting is also induced in children by fright. The young Orang and Chimpanzee exhibit more emotion than the young Gorilla, which maintains a sullen disposition and a mask-like face.

In my paper on the Chimpanzee (72) I described how the ductless glands have played an important part in moulding the external characters of the Apes and Man. The same remarks apply to the Orang, but it must be emphasised that the Orang takes longer to arrive at maturity than the Chimpanzee, which matures more rapidly than the child. The ductless glands are influenced by climatic factors acting from without, and by dietetic factors operating from within. The effects of diet on these glands have been the subject of many papers in physiological journals for some years past, but comparatively little has been written about the action of environmental stimuli.

The Orang, Chimpanzee, and Gibbons are brachiating Apes, and the forearm is longer than the arm. But Weber (83) points out that the great length of the arms in the Gibbon is of post-embryonal development. Gregory (31) thinks that brachiation in the Orang and Chimpanzee was acquired after they arose

\* Atti Acc. Lincei, xiv. p. 706, and Arch. Ital. Biol. xliv. p. 39.

from ancestral forms in the Siwalik Region in Northern India. Wallace (80) thinks that the limb muscles in the young Orang are strengthened as the result of the animal's habit of clinging to its mother's body.

In the young Ape the cranial part of the skull predominates over the facial skeleton. As age advances, the jaws become increasingly prognathous, and continue to develop after the cranium stops growing. In the Gorilla, Chimpanzee, and Gibbon a time comes when the cranial characters become fixed; but the skull of the Orang keeps changing throughout life, thus making classification a difficult process. The female skull may assume male characters and *vice versa*. Variations in the skull have been studied by Brühl (10), Dumortier (22, 23), and others.

The most characteristic feature in the skull of the Orang is the hollowed out or "simognathic" appearance of the face. It varies in degree, as a series of Orang skulls exhibit considerable differences in profile. Simognathism also exists to a slight extent in the other Apes. It is also present in some domestic dogs, such as the Pekinese and Bulldog (Pl. IV. fig. A). In the disease in Man, known as achondroplasia, a similar condition occurs.

The external ears, as have frequently been pointed out, are more degenerate in the Orang than in the other Apes and Man. And the Chimpanzee has the least degenerate ears. Pocock (57) pointed out that the Chimpanzee and Gibbon, which are timid creatures, have larger ears than the Orang and Gorilla, for they require an acute sense of hearing to warn them of the approach of enemies. The Orang lives under sheltered conditions and escapes many dangers; but the Gorilla is well equipped with his great canine teeth and powerful muscles to defend himself against any enemy.

In a previous paper (72) I showed that the power of upward movement of the eyeballs is relatively greater in the Chimpanzee than in Man, and I observed a similar condition in the Orang. The Apes have the power of convergence, but it cannot be sustained for a long time. The eyeballs are relatively larger in the small Gibbon than in the large Apes. Large eyes are associated with nocturnal habits in the Lemurs and *Tarsius*. The ophthalmoscope shows that the fundus oculi in the Apes is similar to that in Man (41). The pigmentation of the conjunctiva exhibits individual variations in intensity.

It has often been pointed out that the external nose of the Gorilla, with its large alar folds, is most like that of Man, but it has no tip, which is the human characteristic.

The lips are bulged forwards by the prognathous jaws, and they do not turn outwards so as to expose the pigmented margins as in Man.

The neck is short in the Apes, and the head is well set between the shoulders, so that it does not interfere with the use of the arms in the brachiators. The head is more mobile in the

Chimpanzee than in the Gorilla. In the human fœtus the neck is very short.

The forearm is longer than the arm in the Orang and Gibbon, but it is frequently stated that the forearm is longer than the arm in the Orang, Gibbon, and Chimpanzee, whereas the reverse is the case in the Gorilla and Man. That relation is not true, however, in the case of the Chimpanzees examined by myself, as can be seen in the following table. The figures are inches.

		<i>Arm.</i>	<i>Forearm.</i>	<i>Hand.</i>	<i>Relation of hand to upper extremity.</i>	
Man	....	12.0	9.5	7.0	Less than	25 $\frac{1}{10}$ .
Gorilla	....	9.0	8.0	6.5	Exceeds	25 $\frac{1}{10}$ .
Chimpanzees*						
No. 1 (♂)	.	6.0	6.0	7.75	"	"
No. 2 (♀)	.	9.3	9.2	7.2	"	"
No. 3 (♂)	.....	8.5	9.75	8.0	"	"
No. 4 (♂)	.	9.5	9.5	8.0	"	"
Orang	.	7.0	7.25	6.0	"	"
Gibbons	.	7.0	8.25	5.25	"	"

In achondroplasia the upper segment of the human extremity becomes shortened, so that the forearm is longer than the arm.

When the human and simian hands are compared, differences are observed in the general physiological characters and in the structure of each of the component structures. The human hand is the only perfect hand. It has a large and perfectly opposable thumb; and it can encircle a sphere. The simian hand has a poor thumb; and it cannot encircle a sphere. It can grasp a cylinder, as it is adapted for swinging on branches. Man can oppose the tips of his thumb and little finger till they touch. But the Apes cannot do this, nor can they close the hand and point with the extended index finger.

The flexure grooves and papillary ridges on the palms exhibit differences. In Man there are grooves running proximo-distally, and two or more grooves run obliquely across the distal part of the palm from the radial to the ulnar side.

In the Apes there are also proximo-distal grooves, but the oblique lines are replaced by transverse ones. There is a wide range of variation in the grooves in both Man and the Apes.

The papillary ridges are most complex in Man. No Ape has a whorl on the terminal phalanges as in many men. The Ape has a loop on each terminal phalanx, and it has fewer ridges in the loop than in Man. Full details of the ridge patterns are contained in the works of Wood Jones (85) and Schlaginhaufen (64).

The epidermis is thickened where it has to bear weight or pressure. In the Apes it forms callosities on the backs of the penultimate phalanges when these are employed in locomotion.

\* These Chimpanzees are arranged in order from the smallest (No. 1) to the largest (No. 2).



In Man the thickenings occur on the palms, and they are best marked in manual workers. When a manual worker stops work for a time the thickenings diminish.

The myological differences are shown in the following table:—

	MAN.	GORILLA.	CHIM- PANZEE.	ORANG.	GIBBON.
Outer head of flexor brevis pollicis }	+	+	+	+	+
Inner head of flexor brevis pollicis ... }	+	0	+	+	+
Flexor longus pollicis }	good separate.	rudimentary not separate.	rudimentary not separate.	rudimentary not separate.	rudimentary not separate.
Adductor obliquus pollicis . . . . . }	+	+	+	+	0
Adductor transversus pollicis . . . . . }	+	+	+	+	+
Other contrahentes ...	0	0	2	0	2
Palmar interossei ..	3	3	6	3	3
Dorsal „ ..	4	4	4	4	4
Insertion of:—					
extensor ossis meta- carpi pollicis . . }	M.P.*	M.P.	sesamoid and trapezium.	M.P. and sesamoid.	sesamoid.
extensor primi inter- nodii pollicis ... }	P. 1 †	M.P.P. 1	M.P. or P. 1	M.P.	M.P.
extensor secundi in- ternodii pollicis.. }	P. 2 ‡	P. 2	P. 1 or P. 2	P. 2	P. 2
Slip connecting first and second lumbrici cales ... . . . . }	0	0	+	0	0

\* M.P. = metacarpal bone of pollex.

† P. 1 = first phalanx.

‡ P. 2 = second phalanx.

The palmar arterial arches exhibit differences. The deep arch is always well developed. The superficial arch is well developed in Man and the Orang; it is slender in the Chimpanzee and it is absent in the Gorilla. Duckworth (20) and Manners Smith (69) believe the superficial arch is absent because the forelimb has not yet lost the power of supporting the body in progression.

The median and ulnar nerves show differences in detail in their cutaneous and muscular distribution.

The metacarpal bones and phalanges are relatively longer, thinner, and more curved than in Man, and they are more equal; that is to say, the metacarpals do not diminish much in size from 2 to 5 as they do in Man.

Goodsir (30) described the axes of the metacarpo-phalangeal joints in the Apes, and showed how their direction helps Man to grasp a sphere, whereas they only permit the Apes to grasp a cylinder.

It can thus be seen that there are numerous small morphological differences in the hands of the Apes and Man, but they alone are not enough to explain why the functions of the human hand are of a much higher order than those of the simian hand. The secret is to be found in the neopallium of the brain. The human hand has been freed from the task of supporting the body, and it has become the servant of the most highly-developed brain in the animal kingdom. Its sensory functions have been enabled to become highly developed. Goodsir pointed out that the hand, the eye, and the muscular sense of the whole upper limb are "the principal organical means by which the human intelligence reaches those motions of external objects, which, when thought under the conditions of Space, enable it to frame its conceptions of external nature."

When a line is drawn through the anterior ends of the ischial tuberosities in the female it passes as follows :—

1. Man ..... between the anus and vulva.
2. Gibbon ..... through the vagina.
3. Orang ..... in front of the vulva.
4. Chimpanzee ..... " " " "

I have not been able to examine this line in the Gorilla. But it is evident that the Gibbon makes a closer approach to Man than the Orang or Chimpanzee.

The urethra opens on the surface of the vestibule in Man. In the human foetus it opens into the urogenital canal. And it opens into the vagina in the Apes. So they retain a more foetal character than Man.

It has been shown by Deniker (18), Bolk, Sperino (73), and myself (72) that Man retains foetal characters in the possession of a mons veneris and well-marked labia majora. And he agrees with *Tarsius* in that respect. In the Apes these structures are well developed in the foetus and young animal, and reduced in the adult\*. The simian clitoris is cylindrical, or shows traces of a bilateral origin. The penis is small in the Apes, and the Orang and Chimpanzee have no glans. The Gorilla and Gibbon have a good or small glans. Man differs from all the Apes in the absence of the os penis.

When the bones of the foot and ankle in the Apes are compared with those in Man, it is seen that the Apes deviate from Man in the order Gorilla, Chimpanzee, and Orang.

When the Ape uses its foot for grasping, the slope of the metatarso-phalangeal joints, running as they do towards the hallux, facilitate a hand-like action. In Man the slope is towards the fibular aspect of the foot, and the line of pressure from above acts in the same direction. This gives width to the foot. The basal line, as regards the action of the pedal interossei, runs through the second digit in Man and the Gorilla; but it passes

\* Sonntag, C. F., 'The Morphology and Evolution of the Apes and Man,' 1924, pp. 268 and 269.

through the third digit, as in a hand, in the Orang, Gibbon, and Chimpanzee.

The muscles of expression in Man differ from those in the Apes as follows:—1. The muscles are shorter and more vertical; 2. The nasal muscles are better developed; 3. The zygomaticus major is frequently more separate; 4. The risorius is better differentiated; 4. The triangularis and auricular muscles are more constant. The Orang and Chimpanzee exhibit their emotions more than the sullen Gorilla; but any attempt to smile results only in grimaces.

Owing to the prognathism of the jaws, the palatine muscles are more horizontal than in Man, and the facial and lingual muscles are longer. The size of the anterior bellies of the digastric muscles is inversely proportional to that of the jaws (Duckworth). The Orang, whose jaws are very massive, has no anterior digastric bellies; and the mylo-hyoid muscle, which supports the tongue, has a more intricate interlacement of fibres than that in any other Anthropoid.

The Apes, like the Monkeys, have an omo trachelian. This muscle is usually absent in Man; but it occasionally appears, when it is to be regarded as a vestigial structure. The omo-hyoid and levator anguli scapulæ exhibit many individual variations. The cervical origin of the trapezius is short, particularly in the Gibbons.

There are many individual variations in the elements composing the erector spinæ in the Apes (see p. 364). Some fibres are attached to the mastoid process in the Gorilla, and Owen (52) stated that the presence of a mastoid process would alone show that that Ape is occasionally erect.

Weber and Goodsir (30) pointed out that in Man the vertebral column with its articular processes and its covering ligaments and muscles forms a spiral, which enables him to maintain an erect posture; and this arrangement is absent in the Apes. Moreover, Man employs less muscular work in locomotion. All he has to do is to bend his body forwards and then bring his pelvis forwards by muscular action, the exertion requisite to do which is determined by the peculiar pendulum-like movements of the lower limbs.

In Man the positions of the anterior superior iliac spine, the ischial tuberosity, and the pubic symphysis are distinctive. They form the basal points of a pyramid whose sides are the sartorius, gracilis, and semi-tendinosus. These muscles combine with the characters of the pelvis, the ilio-femoral ligament, and the long, oblique femoral neck to keep the body erect. In the Apes the muscles are for progression, and they have a more or less extensive attachment to the fascia over the leg.

In the Orang and Gibbons the communication between the tunica vaginalis testis and the abdominal cavity remains open, but it closes in Man, the Gorilla, and Chimpanzee.

The employment of the hallux as a thumb is facilitated by the

splitting of the *tibialis anticus* into two muscles, the modification of the innermost belly of the *extensor longus digitorum*, the characters of the adductor muscles, and the state of the metatarso-phalangeal joint. The division of the *tibialis anticus* is least in the Gorilla.

The skull is bound to the vertebral column by strong ligaments and membranes; and these are more numerous and complex in the Orang than in the Chimpanzee. The *ligamenta subflava* are very elastic in the Gibbons, and are of great assistance during the animal's long leaps. The pelvic ligaments are stronger in the Chimpanzee than in the Orang, as might be supposed from a study of their habits.

The ligaments of the shoulder girdle are relatively stronger in the Orang than in Man.

The external semilunar cartilage is crescentic in Man and the Orang; but it forms a complete circle in the Gorilla and Chimpanzee.

The organs of circulation differ in some respects from those in Man. The heart is, relatively to the size of the body, smaller in the Apes than in Man. The interior of the heart is generally similar in all, but there are small differences in the arrangement of the papillary muscles and *chordæ tendinæ*. The pulse is similar in Man and the Chimpanzee (72).

Deniker (18) pointed out that the *ductus arteriosus* in the Apes remains open till the end of the milk dentition, but more work is necessary before this generalization can be made. In Man the *ductus* closes about the tenth day after birth.

Keith (44) and Deniker (18) have made investigations into the arrangements of the branches of the aortic arch. From these records and from my own observations I find that Man, the Gorilla, and some Chimpanzees, *Cebidæ*, *Edentates*, and *Marsupials* have an identical arrangement. In many Chimpanzees, the Orang, and Gibbons the arch only gives off the innominate and left subclavian arteries. Thus Man has a primitive arrangement of the branches.

In the Orang and Chimpanzee there are relatively fewer branches of main arteries than in Man. This is seen in:—

1. The ophthalmic artery.
2. The occipito-auricular trunk.
3. The linguo-facial trunk.
4. The incomplete separation of the two humeral circumflex arteries.
5. The branches of the abdominal aorta.
6. The branches of the external iliac artery.
7. The branches of the hypogastric artery.
8. The branches of the femoral artery.
9. The arteries of the perineum.
10. The poorer hæmorrhoidal vessels.
11. The absence of large arterial anastomoses round joints.
12. One ovarian artery springs from a renal artery.

All these differences would show that Man has a more subdivided arterial system, with a consequently steadier flow of blood to the tissues.

The lymphatic glands are relatively fewer in the Orang and Chimpanzee (72) than in Man, but the examination of animals soon after a meal might reveal more small nodes in the abdomen. These Apes also differ in the sizes and arrangement of the groups of glands in the neck.

The thyroid gland exhibits a considerable range of variation, but the lobes are always thin and flat. The thymus is in this young animal relatively larger than in a child of the same age (3 years). The blood-vessels of the thyroid gland exhibit a considerable range of variation.

The blood gives positive precipitin reactions with that of Man and the other Apes, but the red blood corpuscles are relatively wider than in Man.

The ovaries are relatively larger than in Man. The uterus has no macroscopic division into body and cervix in this young animal. The anterior vaginal wall lodges the meatus urinarius, and the groove on the ventral surface of the clitoris forms part of the wall. The vulva has no vestibule as in Man. The labial parts of the external organs of generation are larger than in adult animals.

The pelvic floor is not complete in this young animal.

The rectum is straight, and its mucosa is not completely folded as in the Chimpanzee.

The larynx differs from that of Man in :—

1. The presence of air-sacs.
2. The form of the thyroid and cricoid cartilages.
3. No cartilages of Santorini or Wrisberg exist.
4. The vocal cords do not project.
5. There is no promontory.
6. There is no oblique arytenoid muscle.
7. The thyro-arytenoid cannot be separated into parts.
8. The vallecula is shallow.

The Orang differs from all Primates in the absence of any subdivision of the lungs. Among Mammals this condition exists in some specimens of *Phascogale* and *Phascogale*, *Bradypus*, and some Cetacea. As the lungs are divided in the Lorises, one cannot say that non-division of the lungs is associated with sluggish habits.

The optic nerve is immense; the facial nerve has no temporal branches, and the vagus nerves differ from those in Man in details. The left sympathetic cord becomes the left splanchnic nerve. The solar plexus has flattened ganglia. Branches of the vagus run as far as the splenic flexure of the colon, but these fibres may be sympathetic nerves which entered the vagus higher up.

The brachial plexus resembles that of Man more than does the

plexus of the other Apes. And the lumbar plexus differs from that in Man in the relatively smaller nerves of origin of many of the nerves. Only two sacral nerves enter into the sacral plexus in all Apes.

The globe of the eye is small and the optic nerve is immense, but I am unable to draw any conclusion from these points till fresh material becomes available. It is well known that the size of the eye varies inversely to that of the body, but there may be other physiological reasons for the conditions of the ocular apparatus in the Orang.

The cuticular scales on the hairs of the Orang are quite unlike those of the other Primates.

Taking the anatomical conditions as a whole, the Orang exhibits primitive, specialized, and retrogressive features.

### PATHOLOGY.

We are ignorant of the diseases from which the Orang suffers in its native haunts, but we have many specimens which show that it is frequently badly injured by falls from trees. Animals in captivity suffer from hepatic, colonic, pulmonary, and blood diseases. The following table shows the causes of death of some Orangs, which lived in the Society's Gardens:—

No.	Date of Death.	Life in Gardens.	Causes of Death.
1.	30. 10. 01	1 year, 4 months.	Hepatic congestion. Jaundice.
2.	13. 10. 02	1 year, 4 months.	Hepatic congestion. Cerebral oedema.
3.	17. 9. 04	5 days.	Jaundice. Pachymeningitis.
4.	20. 6. 07	10 months.	Anæmia.
5.	5. 7. 10	2 years, 1 month.	Bronchitis. Colitis.
6.	5. 8. 12	5 months.	Pneumonia.
7.	29. 7. 16	8 years, 5 months.	Generalized tuberculosis.
8.	6. 7. 23	1 year, 2 months.	Ruptured cerebral artery.

The last-mentioned animal in the above list had been successfully treated during its stay in the Gardens for scabies, nasal catarrh, and carbon-monoxide poisoning.

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## EXPLANATION OF THE PLATES.

## PLATE I.

Fig. A. Heart of the Orang opened from the right side. C.D.V.S., congenital defect in the septum; C.S., coronary sinus; C.T., crista terminalis; F.O., fossa ovalis.

Fig. B. Heart of the Chimpanzee opened from the right side.

## PLATE II.

Fig. A. Heart of the Orang opened from the left side.

Fig. B. Heart of the Chimpanzee opened from the left side.

## PLATE III.

Fig. A. The external generative organs. CL., clitoris; L.Ma. & Mi., labia majora and minora; M.V., mons veneris.

Fig. B. Vertical section through the skull. B.C.A.B., basi-cranial axis; C.C.T.S., cancellous tissue at site of sphenoidal sinus; H.P., hard palate; I.T.B. and M.T.B., inferior and middle turbinate bones; P.T., permanent tooth.

## PLATE IV.

Fig. A. Skulls of the Orang and Pekinese dog.

Fig. B. Hair of the Orang showing cuticular scales.

18. The Status of the Kangaroo Island Kangaroo (*Macropus fuliginosus* Desm.). By FREDERIC WOOD JONES, M.B., B.Sc., F.Z.S.

[Received February 11, 1924 : Read March 18, 1924.]

(Text-figures 1-4.)

On Monday, March 22nd, 1802, when Matthew Flinders stepped ashore on the island which, "in gratitude for so seasonable a supply" of kangaroo meat, he named Kangaroo Island, he made the first recorded acquaintance with the animal subsequently known as *Macropus fuliginosus*. In the account of his voyage\* he says: 'A number of dark-brown kangaroos were seen feeding upon a grass plot by the side of the wood; and our landing gave them no disturbance. I had with me a double-barrelled gun, fitted with a bayonet; and the gentlemen my companions had muskets. It would be difficult to guess how many kangaroos were seen; but I killed ten, and the rest of the party made up the number to thirty-one, taken on board in the course of the day; the least of them weighing sixty-nine, and the largest one hundred and twenty-five pounds. These kangaroos had much resemblance to the large species found in the forest lands of New South Wales; except that their colour was darker, and they were not wholly destitute of fat.'

The kangaroo which provided Flinders and his crew with so seasonable a supply of fresh meat was abundant, was extremely tame, and was like *Macropus giganteus* (the large species of the forest lands of New South Wales), but darker (dark brown) in colour.

The next historical first-hand account of the Kangaroo Island Kangaroo has more interest for the systematic zoologist. Between December 27th, 1802, and February 1st, 1803, Péron visited the same island, which he named Ile Decrès, and recorded his observations at some length.

Of the kangaroos he says† that they were "les plus grandes de la famille singulière des Kangaroos. Plusieurs de ceux de l'île Decrès sont de la hauteur d'un homme et plus, lorsqu'assis sur les jambe de derrière et sur la queue, ils tiennent leur corps perpendiculaire. Favorisée par l'absence de tout ennemi, la multiplication de ces grands quadrupèdes a été considérable dans cette île: ils y forment de nombreux troupeaux. En quelques endroits pas habituellement fréquentés par eux, la terre est tellement

\* 'A Voyage to Terra Australis, 1801-1803.' London, 1814, vol. i. p. 169.

† 'Voyages aux terres Australes,' 1810, p. 76.

foulée qu'on n'y voit pas un brin d'herbe. De larges sentiers, ouverts au milieu des bois, viennent aboutir de tous les points de l'intérieur au rivage de la mer ; ces sentiers, qui se croisent dans tous les sens, sont partout fortement battus : on pourroit croire, en les voyant d'abord, qu'une peuplade nombreuse et active habite dans le voisinage.

"Cette abondance de Kanguroos rendant leur chasse aussi facile que profitable, nous pûmes nous en procurer vingt-sept, qu'on embarqua vivans à bord de notre navire, indépendamment de ceux qui furent tués et mangés par l'équipage. Cette précieuse acquisition ne nous coûta ni munitions ni fatigue : un seul chien, nommé *Spott*, fut notre pourvoyeur : formé par des pêcheurs Anglois à ce genre de chasse, il poursuivoit les Kanguroos ; et lorsqu'il les avoit joints, il les tuoit aussitôt, en leur déchirant les artères jugulaires. Il ne falloit rien moins que la présence et les cris du chasseur pour arracher la victime à une mort certaine. Avec un tel chien, avec une telle méthode de chasse, il n'est pas douteux que plusieurs hommes établis sur l'île Decrès auroient pu se procurer une nourriture abondante : on conçoit même que la race innocent et foible des Kanguroos seroit infailliblement détruite en peu d'années par quelques chiens de l'espèce de celui dont je parle."

From this very graphic account it appears that Péron considered the animal to be the largest of all the kangaroos, that it was extremely abundant, and was easily run down by such a dog as "*Spott*." But far more interesting is the definite statement that no less than twenty-seven were taken on board alive and were spoken of by their captors as being a precious acquisition.

Combining the accounts of the English and French navigators we may be satisfied that a very large kangaroo, in general like *M. giganteus*, but darker brown in colour, was abundant on Kangaroo Island. We may also accept the generalisations that it was very tame, and so slow as to be easily captured by a dog. Of this very large, dark, slow species of kangaroo, Péron took away twenty-seven living specimens ; that some of Péron's specimens reached Paris, and were those which formed the basis of Desmarest's account of *M. fuliginosus* is, I contend, beyond doubt. Of the prominence of the type of this species Desmarest says\* : "Il y a lieu de croire que cette espèce habite l'île Decrès, sur la côte sud de la Nouvelle-Hollande : car Péron dit qu'on y trouve les plus grands kanguroos connus, et que quelques-uns de ceux qu'il y vit étoient de la hauteur d'un homme et plus lorsqu'ils étoient assis sur leurs jambes de derrière." Desmarest proceeds to quote Péron's account of the animal's habits, and concludes by

\* 'Mammalogie, ou description des espèces de Mammifères' par A. G. Desmarest. Première Partie. Paris, 1820, p. 272. Desmarest's work is not available in Adelaide, and I am much indebted to Mr. Charles Hedley for transcribing the quoted passages from a copy in the Library of Sydney.

saying: "Une grande espèce de kangaroo se trouve aux environs du port Jackson, et ne diffère peut-être pas de celle-ci."

Despite the clear account of Péron and the testimony of Desmarest's statement that "Il y a lieu de croire que cette espèce habite l'île Decrès," the subsequent history of *M. fuliginosus* has become strangely confused.

In 1888 Oldfield Thomas, speaking of *M. giganteus* var. *fuliginosus*, says\*: "This is obviously the usual Tasmanian climatic variety of the common kangaroo, and its modifications are just those which might have been expected.

"The original habitat of this form was said to be Kangaroo Island, South Australia, where Desmarest states, but with some doubt, that it was obtained by Péron and Lesueur. This doubt is confirmed by the fact that (*fide* Gould) it does not exist on Kangaroo Island, and by its common occurrence in Tasmania, where those collectors spent a considerable time."

Gould, in 1863, does not appear to doubt that the original specimens of Péron and Lesueur came from Kangaroo Island, but he added that he believed the animal was no longer to be found there. So far as I can ascertain, Gould did not himself visit Kangaroo Island, nor did he have collections made in that locality; not very much value should, therefore, be placed upon his mere statement that he believed *M. fuliginosus* no longer existed on the island. The statement certainly did not deserve to be quoted as a dogmatic assertion that "it does not exist on Kangaroo Island." Krefft, in 1871, followed Gould, and says: "Little is known of this species, which was first discovered by French voyagers on Kangaroo Island, where it is not now to be found." Later writers, such as Ogilby, 1892; Richard Lydekker, 1894; Lucas and Le Souef, 1909; and Angel Cabrera, 1919, do not even mention the possibility of its ever having lived on Kangaroo Island, or of the original specimens having come from there. They one and all assume that the Tasmanian animal is the type of the species and the only representative of it that has ever existed. Yet all the while that Gould's, by no means dogmatic, statement was being copied from book to book and gaining an air of finality in the process, the animal was living on Kangaroo Island, and its pelts were coming regularly into the salerooms of Adelaide, where, instead of being preserved as museum specimens for a permanent memorial of the species, they became absorbed into the fur or the leather trade as the perfection of the pelage dictated.

We may sweep aside Gould's assumption as wholly incorrect. At the time when he penned his disbelief in its existence, the animal was living in thousands on the island. It appears to me that it is unlikely that Oldfield Thomas would have read so much

\* Catalogue of the Marsupialia and Monotremata in the collection of the British Museum. London, 1888, p. 19.

doubt into Desmarest's account of its habitat had he not had the apparent corroboration of Gould's evidence. I think, therefore, that under the circumstances we are justified in saying that no real evidence has been brought forward to show that the large, dark kangaroo, which Péron obtained on Kangaroo Island, was not the animal from which Desmarest described *M. fuliginosus*. Indeed, it is difficult to accept any other conclusion, and I, therefore, assume that the Kangaroo Island kangaroo, and not the Tasmanian kangaroo, is the type of the Kangaroo Brun Enfumé or *Kangurus fuliginosus* of Desmarest.

A consideration of these circumstances justifies a re-examination of the large kangaroo of Kangaroo Island, and to that end I have paid two visits to Flinders Chase, the fauna reserve at the western end of the island, in order to see the animal in a state of nature; and I have obtained skins and skulls of typical specimens. A small series of skulls, for the most part of rather immature animals, is preserved in the South Australian Museum and, with the kind permission of the Director, I have also availed myself of this material.

Apart from the material I have collected, and the few skulls in our local museum, there seems to be very little of this animal (which has been a stock article of commerce for many years) preserved in collections.

A careful examination of the available material shows clearly that the animal is quite distinct from *M. giganteus*, and that it can by no means be regarded merely as an insular variety of that species.

The original description of Desmarest is as follows:—

“*Car. Essent.* Pelage d'un brun fuligineux en dessus, d'un gris clair en dessous: pattes et queue noirâtres: celle-ci fauve en dessous vers sa pointe.

“*Dimens.* (Mâle).

	pied.	pouc.	lig.
“Longueur totale de corps et du la tête ...	4	6	—
“ „ de la tête .....	—	9	—
“ „ de la queue .....	2	3	—

“Femelle d'un cinquième plus petite.

“*Descript.* Pelage d'un brun fuligineux, plus foncé sur le dos que sur ses côtes, cette couleur passant au gris clair sous le cou, la poitrine et le ventre; dehors des oreilles (qui est peu poilu), museau, bout de la queue en dessus et extrémités des quatre pattes noirâtres; oreilles bordées des poils blancs; pointe de la queue fauve en dessous.

“Ces poils, considérés isolément, sont faiblement annelés; ceux de l'extrémité des pattes sont brun-noirâtres, mais terminés de blanc; ceux du dessous du cou sont brun-cendrés à la base, avec l'extrémité blanche: ceux de dessus de la queue sont d'un brun-noir uniforme.

“Dans la mâchoire supérieure, les quatre incisives intermédiaires sont beaucoup plus petites que les latérales.”

It seems obvious that this description applies well to the animal which Flinders said “had much resemblance to the large species found in the forest lands of New South Wales; except that their colour was darker.” It is quite certain that it applies well enough to the animal which lives on Kangaroo Island to-day.

An extended description of the species, written from recently collected material, is as follows:—

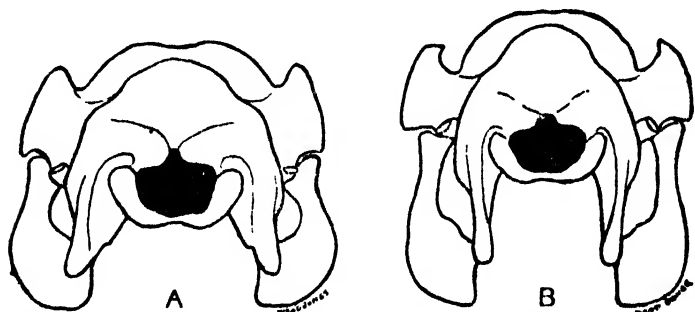
Size large, the adult males being considerably larger and more heavily built than even the largest specimens of *M. giganteus*. Form robust, even clumsy, the old males appearing as almost gigantic lumbering creatures. Hind limbs and tail somewhat short, and manus extremely large. The general colour is a dull, dark sombre brown: the general coloration being considerably darker than that typical of *M. giganteus*. The fur is devoid of sheen and the appearance might be described as dusty. The mid-dorsal line is considerably darker than the sides of the body. The individual hairs of the mid-dorsal region average 25 mm. in length: they are dark smoky brown at the base and lighter at the tips. At the sides of the body the hairs reach a length of 55 mm. and each hair is dull smoky brown at the base and pale dull brown at the tip. The hairs of the mid-dorsal region are straight: those at the sides of the body are crenated, and give the coat a shaggy appearance.

The shoulders and the costal region are somewhat paler than the region of the sides of the abdomen and loin. The ventral surface of the body is clothed with hair upwards of 40 mm. in length, dark smoky brown at the base and white, dirty white, or pale brown at the tips. The crown of the head, as far forwards as the middle of the eye, is dark brown, being darkest in the middle line. The cheeks somewhat lighter. From the middle of the eye to the extremity of the rhinarium the colour becomes increasingly dark, the muzzle itself being nearly black. The chin is dark, the colour becoming paler further back so that the throat becomes increasingly white by the admixture of pale-tipped hairs. Outer side of the limbs dark brown, conspicuously grizzled with white-tipped hairs; inner side pale brown. A dark patch is rather conspicuous over the region of the elbow. Lower part of fore-arm increasingly dark in colour, the white-tipped hairs ceasing about the middle of the fore-arm. Wrist and manus black.

Hind limbs dull brown. Pes clothed with short hairs, which become paler at the margins of the soles. From the base of the digits onwards to the tips the light brown hairs give way to dark brown and finally to black. The large fourth digit is entirely black.

The tail is enormously thick and relatively short, its great girth being maintained for the greater part of its length. On the dorsal surface the base of the tail is clothed with dark brown body-hairs, this soon gives way to short, closely adpressed, brown hairs which become increasingly dark as they are traced distally. The terminal half, or more, of the dorsal surface and sides of the tail clothed with glossy, closely adpressed, black hairs. The ventral surface of the tail has what almost amounts to a ventral crest of coarse harsh longish hairs of a dirty yellowish-brown colour. The ears are clothed with short dark brown hairs externally and with whitish hairs internally. The rhinarium is hairy to the tip, only a narrow margin of black naked skin surrounding the nostrils. The eyelashes are present on both lids and are black in colour. The facial vibrissæ are sparse and black; none of them measuring more than 60 mm. The claws

Text-figure 1.



Posterior views of skulls of (A) *Macropus fuliginosus* and (B) *Macropus giganteus* to show the difference in form. The skulls are of practically the same basal length and the animals of the same age. Quarter natural size.

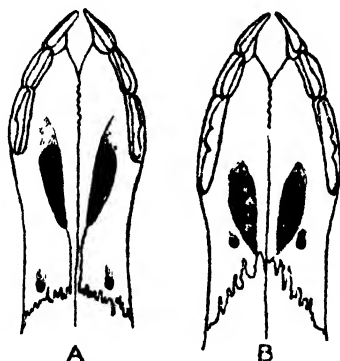
are entirely black; on the manus that of the third digit is 30 mm., and on the pes that of the fourth digit is 35 mm. long. The male differs from the female in being considerably larger and usually somewhat lighter in colour. Old males nearly always have the chest almost white in marked contrast to the black face and extremities.

The skull presents some remarkable and constant characters which serve to distinguish it at once from that of *M. giganteus*. In general, it may be said that the great depth of the posterior portion of the skull and jaws in *M. fuliginosus* readily distinguishes it from the mainland Grey Kangaroo. This distinction is very easily appreciated by an examination of the skulls of the two species, and becomes obvious in a series of measurements. It is illustrated in scale drawing A, text-fig. 1. The posterior nares are considerably lower than they are in *M. giganteus*, the

breadth of the opening exceeding the height, whereas the reverse is usually the case with *M. giganteus*. The external pterygoid processes are shorter, stouter, and more strongly everted than they are in the skull of any other kangaroo with which I am acquainted.

The different species of the large kangaroos differ rather remarkably in a somewhat peculiar point in cranial architecture; for the openings which transmit the anterior palatine nerves have a very variable relation to the incisive canals. In *M. giganteus* these foramina are situated well behind the incisive canals, in *M. rufus* and *M. robustus* the foramina are situated at about the mid-point of the canals; in *M. fuliginosus*, in contrast to *M. giganteus*, they are situated alongside the hind ends of the canals. Moreover, the maxillary-premaxillary suture,

Text-figure 2.



The anterior extremities of the palate and incisor teeth of (A) *Macropus giganteus* and (B) *Macropus fuliginosus*. Half natural size.

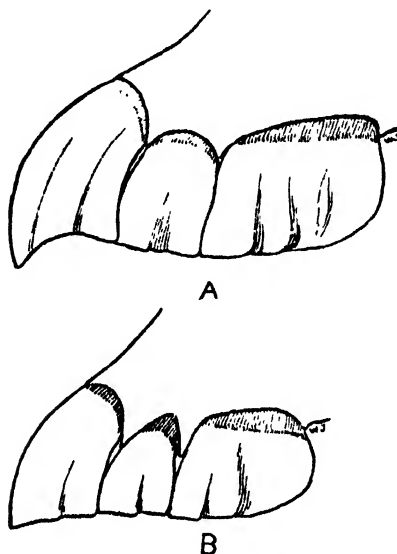
which in *M. giganteus* runs backwards some distance from the incisive canals before it turns laterally across the palate, runs obliquely backwards and outwards from the hind end of the canals in *M. fuliginosus* (see text-figure 2). The nasal bones are relatively short.

These features serve at once to differentiate the skulls of the two species; but, in addition to them, there is the remarkable size and specialization of the last upper incisor tooth, a feature to which Desmarest directed attention. His statement that "dans la mâchoire supérieure, les quatre incisives intermédiaires sont beaucoup plus petites que les latérales" may be rendered more precise by saying that the length of the last incisor exceeds the combined lengths of the two anterior incisors. This great size of the last incisor distinguishes the species from all other kangaroos, for although the last incisor of *M. giganteus* is a



highly specialised tooth it falls considerably short of that of *M. fuliginosus* (see text-fig. 3).

Text-figure 3.



The upper incisor teeth on the labial side of (A) *Macropus fuliginosus* and (B) *Macropus giganteus*. The skulls are of practically the same basal length and the animals of the same age. Natural size.

*Dimensions of Skulls of M. fuliginosus from Kangaroo Island.*

	1	2	3	4	5	6	7
	F.W.J.	S.A. Mus.	F.W.J.	F.W.J.	S.A. Mus.	S.A. Mus.	S.A. Mus.
	♂	no. 1895	♀	♀	no. 1890	no. 1893	♀ no. 1892
Basal length ...	187	102	156	156	152	144	140
Breadth .....	100	92	88	—	85	82	85
Nasals, length ..	72	55	56	53	52	52	55
Palate length ...	125	103	99	101	98	94	92
Diastrama .....	56	42	42	42	41	42	42
Length of I <sup>3</sup> ...	13	12.5	13	13	11	11	11
Width of back of lower jaw .	100	91	90	—	85	84	83

None of these skulls belong to an old adult; in No. 1, the largest of the series, the fourth molar is only just erupting; the remaining skulls are considerably younger.

*Comparative measurements of Skulls of M. giganteus,  
South Australia.*

	G.4	G.5	G.3	G.6 ♂	G.2 ♀	G.7 ♀	G.1 ♂
Basal length ...	177	177	174	172	153	150	112
Ibreadth .....	89	89	85	89	82	76	65
Nasals, length .	71	76	74	70	67	60	44
Palate length ...	116	114	113	113	100	96	70
Diastruma .. ..	57	55	56	51	47	44	27
Length of I <sup>3</sup> ...	11	—	—	11	11	10	10
Width of back of lower jaw .	88	87	81	85	77	74	59

Judging from the dental characters, *M. giganteus* G.4 and G.5 are comparable in age to *M. fuliginosus* No. 1, and *M. giganteus* G.2 to *M. fuliginosus* No. 2.

The animal grows to a very great size, and it is safe to say that no really large specimen has ever been examined by a zoologist. Skull No. 1, with a basal length of 187 mm., belonged to an animal which measured 8 feet 2 inches (2450 mm.) from nose to tail in the flesh. This specimen was not considered to be by any means a large one by men familiar with them, and, since its fourth molar was only just beginning to erupt, it was a fairly young animal. I have seen a living specimen which I believe far exceeded this one. The skin of a typical young male from Flinders Chase has the following dimensions:—

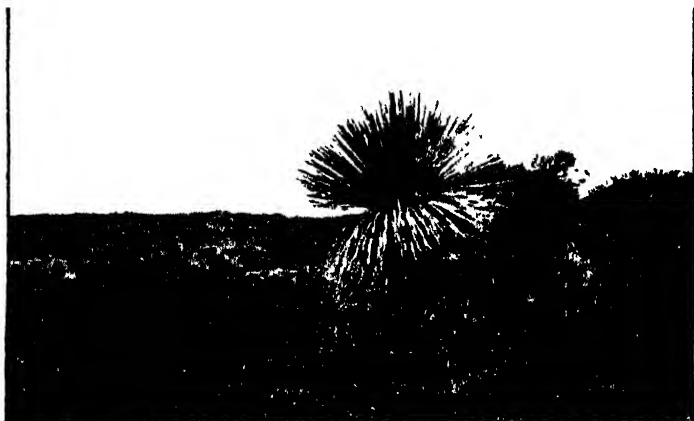
	mm.
Head and body .....	1450
Tail .....	850
Hind foot .....	315
Ear .....	120

Seen in its natural haunts it is a lumbering, rather stupid looking, creature; clumsily built and slow of movement, and with conspicuously large "hands." It must be by far the slowest of all the kangaroos and, as in the days of Péron, it is still easily run down in a comparatively short distance by a very ordinary dog. Many people must have heard, with varying degrees of incredulity, the stories of kangaroos picking up a dog and hurrying with it to the nearest water-hole, wherein they plunge the dog and hold it under till drowned. In the case of *M. fuliginosus* this habit is a very real one, and every season the men who hunt these animals lose dogs in this manner. In the ordinary way, however, this kangaroo is the most gentle, and the quietest, of all its kind. In captivity it shows little of the restlessness which characterizes some species, or of the truculence which characterizes others. It is a placid creature, "innocent et foible" in 1923 as it was in 1802. Upon the western end of Kangaroo Island it lives in the densest bush composed of *Eucalypti* and *Melaleuca* or in the scrubs of *Callistemon* and

*Xanthorrhœa* (see text-fig. 4), and comes out into the open grass-covered spaces to feed. It is by no means strictly nocturnal, and in the thicker parts of the bush it is not particularly shy. As a rule, it is seen either solitary or in pairs; but occasionally small parties congregate in the open grassy places in the island. It breeds only once a year; the young is born as a rule in January and remains in the pouch until October.

*Macropus fuliginosus* still exists in some thousands on Kangaroo Island, and, fortunately, it is probable that quite half the kangaroo population is living on the reserve of Flinders Chase, which consists of some 200 square miles of broken bush-covered country at the western end of the island. This faunal sanctuary is administered by a Board and conserved by a resident Ranger.

Text-figure 4.



Typical habitat of *Macropus fuliginosus*. On right of foreground *Xanthorrhœa* and *Eucalypti*; distant scrub with *Hakea*, *Melaleuca*, and *Callistemon*.

Outside the reserve the legislation only grants the animal partial protection, the open season being from April 1st to September 30th.

During the open season the kangaroo is killed very freely. In 1922 two men slaughtered 600 on a rather limited holding, and during the present season 300 more were killed at the same place. These animals are skinned for the leather trade. Although its tenure of existence appears assured within the sanctuary of Flinders Chase, the indiscriminate slaughter of this fine animal on other parts of the island is much to be deplored. It is hoped that a full measure of protection will one day be accorded to the species throughout the whole of its island home.

19. The Myology of the Tree-Shrew (*Tupaia minor*).

By W. E. LE GROS CLARK, F.R.C.S.Eng., F.Z.S.

[Received January 9, 1924: Read March 4, 1924.]

(Text-figures 1-24.)

The only record that deals in detail with the musculature of the Tree-Shrew is Leche's (8) monograph "Zur Anatomie der Beckenregion bei Insectivoren," where the muscles related to the pelvis are described. Carlsson (2), in order to institute a comparison between *Tupaia* on the one hand and the Insectivora and Prosimiæ on the other, gives brief notes on the muscles. These notes, however, are wanting in detail and, in addition, contain statements which differ curiously from my own findings. Kaudern (5) has dealt with the abdominal muscles of *Tupaia*, showing their remarkable resemblance to those of the Lemuroidea.

With the above exceptions, the literature of the myology of *Tupaia* is limited to a few references to isolated points in papers of a general nature.

It is well known that the anatomy of *Tupaia* is of very peculiar interest, indicating a unique combination of primitive features with primate characters, and, if even for this reason alone, it is considered of great importance that a full and detailed anatomical description of *Tupaia* should be given.

The present paper deals with the skeletal musculature of the Tree-Shrew and the evidence which may be adduced from it regarding the systematic position and affinities of the animal.

With regard to the value of comparative myology for systematic purposes, sufficient attention is not commonly given to this aspect, possibly because of the tacit assumption that muscles are so directly related to the environmental activities of the animal that they readily undergo changes associated with changes in the latter's habits of life. This effect of environment, however, is undoubtedly very much less than is usually supposed. A forcible illustration of this has been given by Parsons (11), who, dealing with comparative mammalian myology, has stated that "the muscles of the arboreal squirrel hardly differ at all from those of the burrowing marmot." Curiously enough, however, he appears surprised at this, and suggests that the Squirrels have not acquired their arboreal activities for a sufficiently long time to produce the assumed "arboreal" changes in the muscles. Against this it may be argued (1) that no such change of even an incipient nature are noted in the Squirrel, and (2) that no observer can doubt that the Squirrel is as completely adapted to its mode of life as is required. From this, it appears that an almost identical arrangement of muscles can be associated

with different modes of life, and that the anatomy of the muscular system may be of considerable taxonomic importance.

Muscle variation among mammalian types takes place more by the disappearance of a muscular element and slight changes in the attachments and intrinsic differentiation of individual muscles rather than by the addition of a new element, and in the manner of the disappearance there are two extremes. In the one case, a muscle element may disappear completely, leaving no trace of its former existence and in quite an inexplicable way—such as the brachioradialis in Insectivores, and, in the other case, a vestigial and apparently useless muscle may persist as an indication of a former more complete development, such as the plantaris and auricular muscles of human anatomy. Both these phenomena are of importance in discussing systematic affinities.

In the case of the Tree-Shrew, we are fortunate in having a "control" which we may use for purposes of comparison in order to ascertain whether some of the peculiar features of the Tupaiidæ may not be in the nature of adaptations to arboreal habits of life. This control is the Squirrel, an animal in no way related to the Tree-Shrew. To anyone who has wandered into jungles in search of Tree-Shrews, the similarity between these animals and Squirrels, in their shape and form, and in the manner of their activities among the branches, is remarkable. It has, indeed, been suggested that we have here an example of animal mimicry. There seems no doubt, then, that so far as concerns their muscular system, the environment of these two animals is almost identical. Now, it may be remarked here that one of the objects of this paper is to institute a comparison between the Tupaiidæ on the one side and the Insectivora and Lemuroidea on the other, with both of which orders the Tree-Shrew shows affinities. Points of resemblance between the muscular anatomy of *Tupaia* and the Lemurs might be claimed as instances of convergence associated with similar arboreal habits, and it is here that the Squirrel will be useful in order to ascertain whether such muscular modifications are invariably correlated with such habits. It may also be pointed out that the various species of the Tupaiidæ differ considerably in the degree of their arboreal activities. The smaller species with relatively longer tails (e. g. *T. minor*) are thoroughly arboreal, and though they are at times seen in the undergrowth a short distance only from the ground, they are frequently found among the higher branches of the large trees. The larger species (e. g. *T. ferruginea*) with relatively shorter tails are much less arboreal. Wood-Jones (14), indeed, refers to these latter as "bush animals." Yet these different species show no corresponding difference in the disposition of their muscles. This will, perhaps, serve to indicate sufficiently conclusively that there is very little question of secondary adaptation to arboreal life as an explanation of some of the primate features found in the muscles of *Tupaia*.

## FACIAL MUSCLES.

*M. Occipito-frontalis*.—The fibres of this muscle take origin from the occipital crest behind, and run forwards along the dorsum of the nose. Posteriorly some of the fibres are detached from the main mass to form two distinct bundles which gain attachment to the concha of the ear, forming a *retrahens aurem*. More anteriorly some fibres take origin from the deep aspect of the helix, and run forward immediately above the eye, partially blending with the *orbicularis oculi* and forming an *attrahens aurem*. Superficially to the posterior part of the muscle a well-marked band of fibres passes from the mid-dorsal line of the nuchal region downwards and laterally behind the ear to the ventral aspect of the neck. This muscular sheet in its course passes superficial to the *platysma* below and behind the ear.

The *Platysma* sheet spreads forwards from the mid-dorsal line of the nuchal region and the lateral and ventral aspects of the neck to the upper and lower lips, blending with the *orbicularis oris*, the uppermost fibres rising from the fascia over the parotid gland. The lower and medial margin of the muscle is well-defined, and in the interval between the two muscles of either side can be seen the *sphincter colli*.

*M. Sphincter colli*.—This consists of a thin sheet of muscle whose fibres cross the ventral aspect of the neck transversely. The most posterior fibres pass up on either side to gain a firm attachment to the lower part of the cartilaginous auditory meatus.

*M. Auriculo-labialis*.—This muscular sheet is apparently derived from the uppermost fibres of the *platysma*, and runs forwards from the anterior part of the auricle to the upper lip and the malar region, the upper fibres passing forwards deep to the *levator labii superioris* to blend anteriorly over the dorsal aspect of the nose with the *frontalis* sheet.

*M. Levator labii superioris*.—A fairly well-defined muscle, derived from the *frontalis* sheet and passing downwards and forwards from just above and in front of the eye to the upper lip, passing superficially to the zygomatic muscles.

*M. Orbicularis oculi*.—This is a well-marked muscle the fibres of which are disposed in the usual circular fashion round the eye.

*M. Zygomatico-orbicularis*.—I have designated by this name a very distinctly circumscribed muscular bundle which rises from the upper margin of the anterior end of the zygomatic arch and is inserted at the posterior angle of the eye into the *orbicularis oculi*. This muscle corresponds possibly to the *post-orbicularis* slips noted (and figured) by Parsons and Windle (12) as occurring in the *Canidæ*. Nothing corresponding to this muscle is mentioned or figured by Dobson in his monograph on the *Insectivora*.

*M. Zygomatici*.—These muscles rise from the malar region

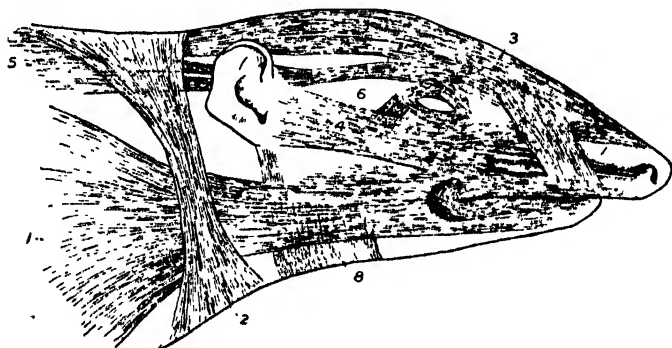
below and in front of the eye, and run forward to the side of the nose. In *T. ferruginea* three well-marked slender tendons are present, but in *T. minor* one tendon only can be demonstrated with certainty on gross dissection.

*M. Erect. vibrissæ*.—This consists of muscle fibres arranged in an antero-posterior direction superficial to and among the zygomatic muscles.

*M. Dilator naris*.—A small muscle bundle, rising from the anterior end of the tendon of the zygomaticus and inserted into the outer wall of the nostril.

*M. Dorso-humeralis et abdomino-humeralis*.—These are both well-marked muscles. The two bundles are quite distinct at their origin, being separated in the axillary region by the external mammary vessels. At their insertion they are not easily separable. The upper part of the abdomino-humeralis tendon is inserted

Text-figure 1.



Tree-Shrew. Facial musculature.

1. Platysma sheet.
2. Superficial "sphincter colli."

3. Occ.-frontalis sheet.
4. Auriculo-labialis.
5. Retraheus aurem.

6. Zygom.-orbic.
7. Lev. labii sup.
8. Sphincter colli.

into the capsule of the shoulder-joint in immediate continuity with the tendon of pectoralis minor. The lower part with the tendon of dorso-humeralis is inserted into the proximal quarter of the humeral shaft lateral to the long head of the biceps by a thin fascial expansion.

The abdomino-humeralis runs backwards and medially to meet its fellow of the opposite side in a median raphe at the lower end of the pectoralis major, forming a sharp and distinct anterior margin which lies superficial to the pectoralis major at the most posterior point of origin of the latter muscle. The margins of pectoralis minor and abdomino-humeralis are in contiguity, except where they are separated by the branch of the medial ant. thoracic nerve passing to pectoralis major.

The dorso-humeralis spreads out over the back and sides of the trunk, reaching posteriorly to the lateral surfaces of the thighs.

Neither of these muscles was traced to the root of the tail. Both muscles are supplied by the medial anterior thoracic nerve.

*M. Trapezius*.—Rises from the occipital protuberance and slightly from the adjacent part of the occipital crest, from the median nuchal raphe, and from all the thoracic spines. It is inserted into the whole length of the upper border of the scapular spine and to the base and medial end of the inferior border. The muscle gains no attachment to the acromion process or clavicle. The insertion to the base of the spine is tendinous as in Man.

*M. Levator scapulæ*.—Rises in conjunction with the insertion of the longus colli from the anterior surface of the body of the atlas. It forms a thick fleshy muscle which is inserted into the lateral margin of the acromion process and outer extremity of the spine of the scapula, slightly overlapping the trapezius superficially. It is supplied by the third cervical nerve.

Text-figure 2.

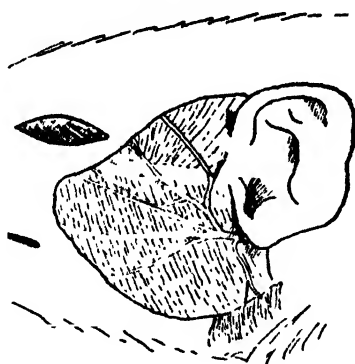


Diagram illustrating the peripheral distribution of the facial nerve.

*M. Rhomboidens capitis*.—One slip rises from the anterior surface of the transverse process of the atlas, the main mass being a thin sheet which rises from the whole length of the occipital crest and from the median raphe for about 5 mm. below, deep to trapezius. Inserted at the medial end of the spine of the scapula and at the vertebral border below as far as the inferior angle, passing deep to rhomboidens cervicis. A few fibres blend with the fascia covering supraspinatus.

*M. Deltoideus*.—Rises from the lateral border of the acromion process deep and anterior to the levator scapulæ, and from the anterior aspect of the lateral half of the clavicle. No origin from the lower border of the spine.

Inserted into the deltoid tuberosity of the humerus. The muscle shows a bipenniform arrangement of its fibres as in Man.

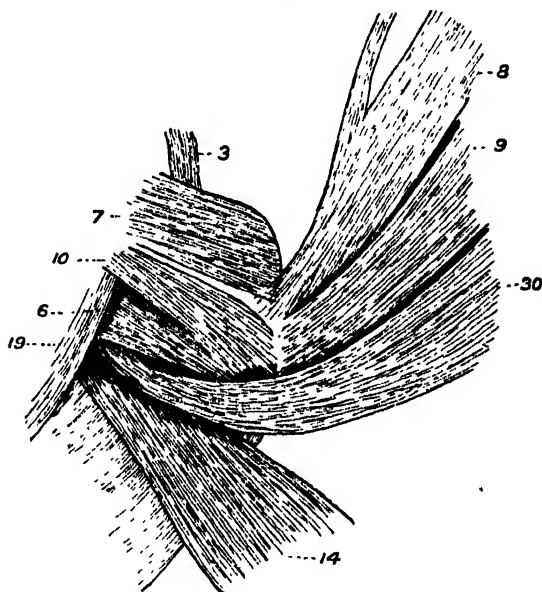
*M. Rhomboideus cervicis*.—A thick muscle, not separable into two elements. Rises above from the median nuchal raphe in



continuity with rhomboideus capitis, and from the first three thoracic spines. Inserted into the vertebral border of the scapula extending from the base of the spine to the inferior angle.

*M. Latissimus dorsi*.—Rises from the lowest seven thoracic spines and the lumbar aponeurosis, gaining no direct attachment to the iliac crest or to the lower ribs. Inserted to the floor of the bicipital groove.

Text-figure 3.



Scapular muscles (left).

- |                   |                    |                           |
|-------------------|--------------------|---------------------------|
| 3. Omo-hyoid.     | 8. Rhomboid. cap.  | 14. Lat. dorsi.           |
| 6. Teres major.   | 9. Rhomboid. coll. | 19. Triceps (outer head). |
| 7. Supraspinatus. | 10. Teres minor.   | 30. Spino-humeralis.      |

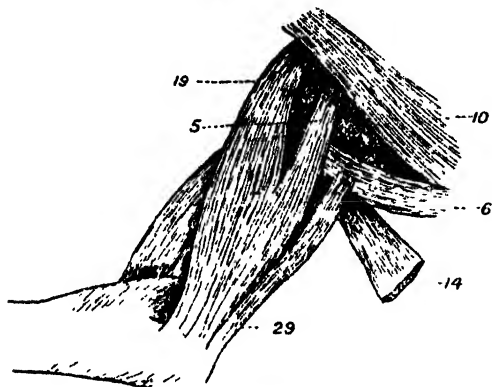
*M. Spino-humeralis*.—I have given this name to a flat muscle which rises from the 2nd to 6th thoracic spines, lying in the same plane as rhomboideus. It runs laterally across the inferior angle of the scapula to blend eventually with the tendon of teres major, and to be inserted with it into the humerus deep to the latissimus dorsi, but easily separable from it. Some fibres of this muscle are inserted into the fascia covering the infra-spinatus. It is supplied by the middle subscapular nerve.

*M. Teres major*.—Rises from the inferior angle and whole length of the axillary border of the scapula, and partly from the fascia covering the subscapularis. Inserted into the medial lip of the bicipital groove. The muscle is supplied by a separate subscapular branch from the posterior cord of the brachial plexus.

*M. Teres minor*.—This muscle is superficial and closely applied to the infraspinatus, concealing the latter muscle completely. It rises from the medial half of the lower border of the spine of the scapula and from the vertebral border below the spine, as well as, to a slight extent, from the fascia covering the infraspinatus. It is inserted into the humerus immediately below the infraspinatus and posterior to the upper end of the lateral head of triceps. It is supplied, as usual, by the axillary nerve.

Carlsson (2) denies the presence of this muscle in *T. javanica*, and thus admits a condition very frequently found among the

Text-figure 4.



Shoulder muscles (left).

5. Triceps (long head).

29. Dorso-epitroch.

(Other references as in text-fig. 3.)

Lipotyphla. I have found it uniformly present in the several specimens of *T. minor* and *T. ferruginea* which I have examined, and I suggest that in the case of *T. javanica*, its close association with the infraspinatus has allowed it to be mistaken for the latter muscle.

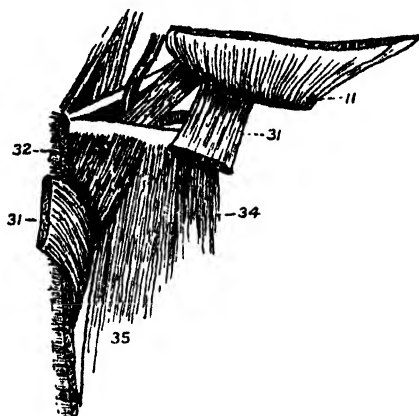
In dealing with rodents, Parsons (10) notes that the teres minor is "especially indistinct in the Sciuromorpha."

*M. Dorso-epitrochlearis*.—This muscle is completely duplicated. One part has the usual origin from the latissimus dorsi, while the other part bears a similar relation to the lower border of the teres major. A few fibres of this second muscle rise from the spinalis dorsi component of the teres major, but most are derived from the teres major muscle itself. Both muscles are inserted independently into the olecranon process of the ulna, the teres major portion lying lateral to the portion derived from the latissimus dorsi. Both muscles are supplied from the branch of the musculo-spiral nerve passing to the long head of the triceps.

In connection with this duplication of the dorso-epitrochlearis, Parsons (13) notes an extra origin of the muscle from teres major in *Tatusia*, and additional slips from the scapula and

teres major in *Orycteropus*, but there is no indication in these cases of two completely separate muscles. Duckworth notes the origin of the muscle by two heads from both sides of the latissimus dorsi in *Lemur*, and I have myself confirmed this point. Carlsson (2) implies that the Lemuridæ agree with *Tupaia* in the conformation of this muscle, but I have never found any portion of the muscle taking origin from the teres major in *Galago*, *Nycticebus*, or *Lemur*, while Murie and Mivart in their work (9) make no mention of it. It is suggested also that the double condition of the dorso-epitrochlearis in *Tupaia* is associated directly with arboreal habits. This argument is nullified by the simple condition of the muscle found in many animals which are clearly more arboreal than the Tree-Shrew, while this is also the case in many cursorial mammals.

Text-figure 5.



Pectoral region (left). The pectoral muscles cut and reflected.

- |                  |                        |                       |
|------------------|------------------------|-----------------------|
| 11. Pect. major. | 32. Sterno-costalis.   | 35. Rectus abdominis. |
| 31. Pect. minor. | 34. Scalenus posticus. |                       |

*M. Supraspinatus*.—Rises from the supraspinous fossa, and is inserted into the great tuberosity of the humerus.

*M. Infraspinatus*.—Rises from the infraspinous fossa, lying deep to and wholly concealed by the teres minor. Inserted into the humerus below the preceding muscle.

*M. Subscapularis*.—This is a thick muscle, rising from the subscapular fossa and showing 4 or 5 tendinous intersections which make well-marked "costæ" on the scapula. Inserted into the lesser tuberosity.

*M. Pectoralis major*.—Rises from the side of the whole length of the sternum and xiphisternum, its distal end being overlapped by the abdomino-humeralis and (to a very slight extent) by the transversus abdominis. No clavicular origin. Inserted into the outer lip of the bicipital groove, sending an expansion

proximally to blend with the capsule of the shoulder-joint. At the insertion of the muscle the lower fibres tend to pass upwards deep to the upper fibres. The branch of the medial anterior thoracic nerve which supplies the pectoralis major passes to the muscle partly by piercing the pectoralis minor and partly by running between pectoralis minor and the abdomino-humeralis.

*M. Pectoralis minor*.—Rises from the 2nd to 6th costal cartilages, close to the sternal margin. Inserted into the capsule of the shoulder-joint. No attachment to the coracoid process (contrary to what was noted by Lander (7)).

*M. Sternocostalis*.—This muscle lies deep to pectoralis minor, rises from the 2nd, 3rd, and 4th costal cartilages, and is inserted into the anterior border of the 1st rib.

*M. Subclavius*.—A well-marked muscle, rising from the medial end of the upper surface of the first rib and costal cartilage and inserted into the posterior and inferior aspect of the lateral half of the clavicle. A few fibres also gain attachment to the coraco-clavicular ligaments at their upper end.

*M. Coraco-brachialis*.—Rises from the tip of the coracoid process.

- (1) *Pars brevis*.—A rounded muscular band winding close to the neck of the humerus, to be inserted into the inner lip of the bicipital groove immediately above the insertion of latissimus dorsi.
- (2) *Pars longa*.—Inserted into the humeral shaft immediately below the insertion of latissimus dorsi and into the medial intermuscular septum. A further accession of muscular fibres occurs at the lower end of the intermuscular septum which run down superficial to the median nerve to reach the medial epicondyle. The musculo-cutaneous nerve passes entirely deep to the *pars longus*.

It is to be noted that part or whole of this muscle is frequently absent among the Insectivora.

#### *M. Biceps*.—

- (1) Long head.—Rises from the supraglenoid tubercle, the tendon passing through the capsule of the shoulder-joint, but not lying free within the joint cavity.
- (2) Short head.—A slender but quite distinct muscle-band rising from the coracoid process.

Insertion into the radial tubercle. No *lacertus fibrosus* present.

The presence of a well-marked short head is in contrast to its quite common absence among the Insectivora. In the *Sciuromorpha*, Parsons (10) notes that the short head is only represented by the fibres rising from the front of the coraco-brachialis.

*M. Brachialis anticus*.—This muscle is divisible into medial and lateral components. The former rises from the anterior

surface of the humerus as far proximally as the deltoid insertion, and partly from this insertion itself. The latter takes origin from the humeral shaft lateral to the deltoid, deep to the lateral head of the triceps as far up as the insertion of *teres minor*.

Inserted into the coronoid process of the ulna.

*M. Triceps*.—This muscle consists of the following parts:—

- (1) Long head.—Rising from the infraglenoid tubercle.
- (2) Medial head.—A thin strip of muscle rising from the humeral shaft as far up as the level of the insertion of *teres major*.
- (3) Lateral head.—A bulky mass, divided into two distinct parts: (a) superficial, which rises from the neck of the humerus deep to the insertion of *teres minor* and above *brachialis anticus*; (b) deep, rising from the posterior surface of the humerus above the musculo-spiral groove, and corresponding to the lateral head of human anatomy. The greater part of the triceps is inserted into the proximal end of the olecranon process. The superficial portion of the lateral head, however, is attached by an expansion to the lateral border of the olecranon. The double condition of the lateral head of triceps is of importance. The upper part only (rising from the neck of the humerus) appears to be represented in the *Lipotyphla* (Dobson) and in the *Sciuro-morpha* (Parsons). Both parts are present, as I have been able to satisfy myself, in *Lemur*.

*M. Anconeus*.—This does not form a distinct muscle, but is represented by the distal fibres of the medial head of the triceps. It is inserted into the proximal end only of the lateral aspect of the olecranon process.

*M. Condyllo-olecranon*.—A narrow thick band of muscle, rising from the lower end of the medial supracondylar ridge and inserted into the olecranon process. The lower border of the muscle is in contact with the upper fibres of *flexor carpi ulnaris*.

*M. Brachioradialis*.—This muscle rises from the proximal end of the lateral supracondylar ridge and from the fascia on the deep aspect of *ext. carpi rad. long.* It is inserted as usual into the lateral aspect of the lower end of the radius 1 mm. above the base of the styloid process. Carlsson states that this muscle is absent in *Tupaia*. It is well developed, however, in all the specimens of *T. minor* and *T. ferruginea* which I have dissected. I regard this as of considerable importance, for this muscle is commonly completely absent in the Insectivora.

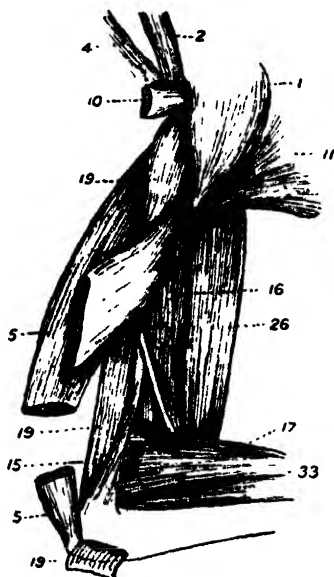
*M. Extensor carpi radialis longus*.—Rises from the lateral supracondylar ridge for an extent of 4 mm. Inserted into the base of the second metacarpal bone.

*M. Extensor carpi radialis brevis*.—Rises from the lateral epicondyle and inserted into the base of the third metacarpal. This muscle has a well-developed belly.

*M. Extensor communis digitorum*.—Rises from the lateral epi-

condyle and deep fascia. It possesses a comparatively short muscle-belly, which terminates in a variety of ways eventually to supply the ulnar four digits, forming an expansion on the dorsum of the digits to gain insertion into the middle and terminal phalanges. In one specimen (No. 6) one long tendon was formed, which split up into its four component parts at the level of the wrist-joint. In another specimen (No. 5) the muscular belly divided to form three long tendons, each of which at the wrist-joint divided again into two. The inner tendon then supplied digits 2 and 3, the middle digits 3 and 4, and the outer digits 4 and 5.

Text-figure 6.



Muscles of upper arm (right).

- |                          |                           |                           |
|--------------------------|---------------------------|---------------------------|
| 1. Deltoid.              | 11. Pect. major.          | 19. Triceps (outer head). |
| 2. Lev. scap.            | 15. Triceps (inner head). | 26. Biceps.               |
| 4. Trapezius.            | 16. Brach. ant.           | 33. Ext. c. rad. long.    |
| 5. Triceps (outer head). | 17. Brachiorad.           |                           |

*M. Extensor digitorum lateralis*.—Rises from the lateral epicondyle in conjunction with the preceding muscle. It forms a long tendon, which at the level of the wrist-joint divides into two parts, running to digits 4 and 5 and fusing with the corresponding tendons of the extensor communis digitorum.

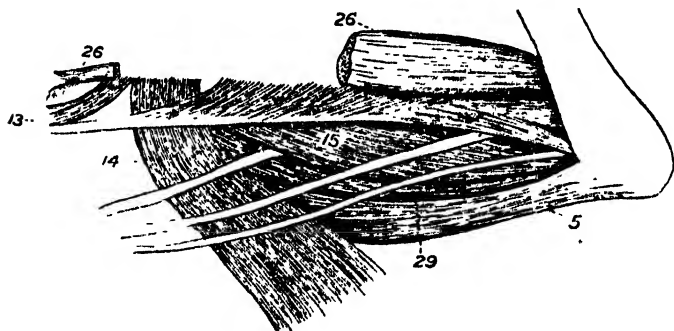
*M. Extensor carpi ulnaris*.—Rises from the lateral epicondyle and the olecranon process. No direct attachment to the posterior ulnar border. Inserted into the base of the fifth metacarpal.

*M. Abductor pollicis*.—This is a double muscle, rising from the posterior surfaces of the upper three-quarters of the radius and

ulna and a corresponding extent of the interosseous membrane. Below it forms two tendons, both of which are inserted into the radial side of the base of the first metacarpal.

*M. Extensor profundus*.—Rises from the postero-lateral surface of the ulna medial to and above the upper end of abductor pollicis and deep to ext. carpi ulnaris. In one specimen it was found to divide to form two long tendons, of which the radial supplied the pollex, while the ulnar divided again on the back of the wrist to supply the 2nd, 3rd, and 4th digits. In another specimen one long tendon only was formed, dividing at the wrist to supply the radial three digits. The tendons pass superficial to those of the carpal extensors. The tendon to the pollex gains attachment to the bases of the proximal and terminal phalanges. The tendons to the other digits blend with the corresponding tendons of the superficial extensor.

Text-figure 7.



Medial side of upper arm (left).

13. Coraco-brachialis. 14. Lat. dorsi. 29. Dorso-epitroch.

(Other references as in text-fig. 6.)

*M. Supinator*.—Rises from the lateral epicondyle, adjacent to part of the coronoid process of the ulna and the lateral aspect of the capsule of the elbow-joint. Inserted into the anterior and lateral aspects of the upper end of the radial shaft. The posterior interosseous nerve passes entirely deep to the muscle, the latter not being divisible into two laminæ.

*M. Pronator radii teres*.—Origin from the medial epicondyle, extending to a slight extent on to the medial supracondylar-ridge. Inserted by a broad thin expansion to the middle of the lateral aspect of the radial shaft. Wood-Jones asserts that the deep head is present in *T. ferruginea*, but I have not been able to find any trace of it in my specimens of this animal or in *T. minor*. Herein my observations agree with those of Kloster (8).

*M. Palmaris longus*.—Rises mostly from the deep fascia of the forearm, the origin extending proximally to the medial epicondyle. The muscle possesses a well-developed belly, which becomes tendinous in the distal third of the forearm. At the wrist it

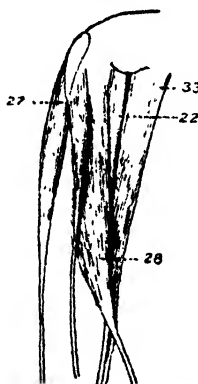
broadens out to form the palmar fascia. The latter is not very well defined, except laterally, where it gains a strong attachment to the lateral side of the base of the first metacarpal.

*M. Flexor carpi radialis*.—Rises from the medial epicondyle and deep fascia. Inserted into the base of the second metacarpal.

*M. Flexor carpi ulnaris*.—Rises from the medial epicondyle, medial margin of the olecranon process, and middle third of the posterior border of the ulna. Inserted into the pisiform bone.

*M. Flexor sublimis digitorum*.—Rises from the medial epicondyle and deep fascia. No radial head present. Divides into three tendons, which supply the 2nd, 3rd, and 4th digits. At the wrist-joint it gives off a thick tendon from its deep aspect to join the tendons of flexor profundus.

Text-figure 8.



Deep extensor muscles of forearm (right).

22. Supinator.

28. Abd. poll.

27. Ext. profundus.

33. Ext. c. rad. long.

*M. Flexor profundus digitorum*.—This muscle can be divided into two parts:—

- (1) Superficial—rising from the medial epicondyle.
- (2) Deep—which rises from the radius, interosseous membrane, and ulna. This part may be divided in a general way into three parts:—
  - (a) A radial head which rises from the anterior surface of the radius, extending from the bicipital tubercle down almost to pronator quadratus.
  - (b) A central head which rises from the interosseous membrane and the contiguous borders of the radius and ulna, extending up medially to the insertion of brachialis anticus.
  - (c) An ulnar head which rises from the medial surface of the ulna, reaching to the base of the olecranon process above.



Near the wrist the tendons of the deep flexor are joined by a thick tendon from flexor sublimis digitorum. The tendons supply all the digits. The tendon to the pollex appears to be derived mainly from the superficial part and the radial head of the deep part of the muscle. The tendon derived from the flexor sublimis runs mainly to the ulnar digits. The superficial part is supplied direct from the median nerve. The deep part is supplied on the radial side by the volar interosseous and on the ulnar side by the ulnar nerve.

*M. Palmaris brevis*.—A well-developed bundle of muscle fibres runs transversely across the palm to the hypothenar eminence,

Text-figure 9.

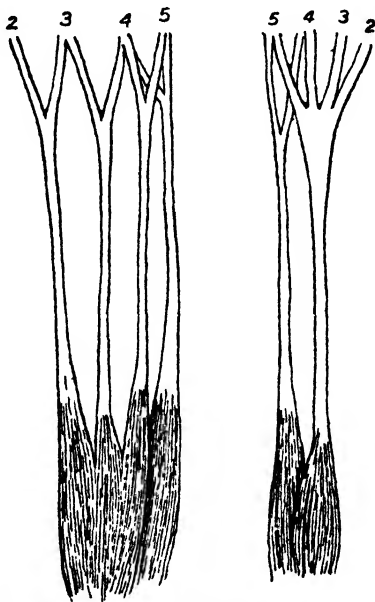


Diagram illustrating alternative arrangements of the tendons of  
ext. com. digit. and ext. digit. lat.

and occupies the same position and relations as the human palmaris brevis.

Carlsson denies the presence of palmaris brevis in *Tupaia*, but describes a similar muscle designated "Carpalballenmuskeln."

*M. Pronator quadratus*.—A feebly-developed muscle which runs between the opposed borders of the lower quarter of the radius and ulna.

*M. Flexor brevis manus*.—A small muscle, rising largely from the anterior annular ligament of the wrist at its ulnar side, and supplying a perforated tendon bearing the same relation to the 5th digit as do the tendons of flexor sublimis digitorum to the

other digits. The presence of this muscle may be regarded as a primitive character.

*M. Abductor minimi digiti*.—This is a broad muscle, rising from the ventral and dorsal aspects of the pisiform and inserted into the ulnar side of the base of the proximal phalanx.

*M. Flexor brevis minimi digiti*.—A well-developed muscle rising from the anterior annular ligament close to the pisiform. Inserted into the ulnar side of the base of the proximal phalanx.

*M. Opponens*.—Not present.

*M. Abductor pollicis brevis*.—Rises from the scaphoid, trapezium, and lateral side of the proximal half of the first metacarpal, as well as from the anterior annular ligament. This muscle can be somewhat indefinitely divided into two parts, superficial and deep. Both are inserted into the radial side of the base of the proximal phalanx of the pollex, while a few fibres of the deep part gain attachment to the radial margin of the distal end of the first metacarpal, and perhaps represent an opponens pollicis.

*M. Flexor brevis pollicis*.—This muscle, which is well-developed, takes origin from the scaphoid, the anterior annular ligament, and the palmar fascia. Inserted into both sides of the base of the proximal phalanx.

*M. Opponens pollicis*.—Not present, unless represented by some fibres of the abductor pollicis brevis as described above.

The *Anterior annular ligament* is a relatively feeble fascial band attached mainly to the scaphoid and pisiform bones.

*M. Lumbricales*.—These are four in number. The first rises from the radial side of the profundus tendon supplying the index. The remainder rise from the contiguous margins of their corresponding tendons. The muscles are inserted mainly into the bases of the proximal phalanges.

*M. Adductor pollicis*.—Rises from the carpal ligaments at the base of the second and third metacarpals. Inserted into the ulnar side of the base of the proximal phalanx of the pollex.

*M. Interossei*.—These may be divided into three palmar and four dorsal muscles, though they all lie on the palmar aspect of the metacarpus. The palmar interossei rise from the ventral aspect of the carpus only, and are related at their insertions to the radial side of the 4th and 5th digits and the ulnar side of the 2nd digit.

The dorsal interossei rise from the sides of the metacarpals as in Man, and also to a large extent from the volar aspect of the carpus. The 2nd and 3rd dorsal interossei rise by a single narrow belly which lies on the palmar aspect of the 3rd metacarpal, splitting to pass to insertions on either side of the 3rd metacarpophalangeal joint.

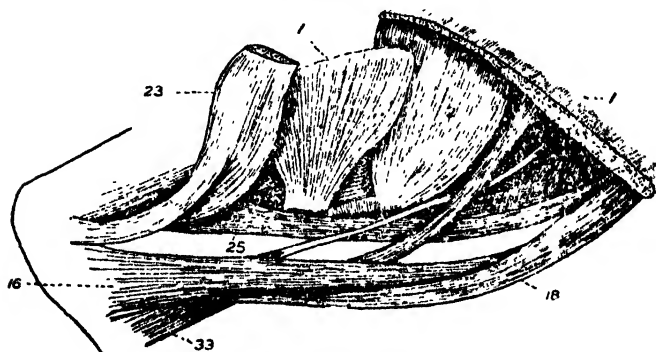
*M. Gluteus maximus*.—This muscle is a thin lamina, of which the anterior margin is thick and rounded. Rises from a small part of the iliac crest, from the lumbo-dorsal fascia, and from the sacral spines. The anterior fibres are inserted into the fascia lata, and clearly represent the tensor fasciæ femoris muscle, being

supplied by the superior gluteal nerve. These are not clearly differentiated from the posterior fibres which gain attachment to the third trochanter.

*M. Femorococcygeus*.—This muscle is not separable from the preceding muscle. It rises from the 1st, 2nd, and 3rd caudal transverse processes, and, forming a thick muscular band, passes down to its insertion into the lower half of the lateral aspect of the femoral shaft, starting from immediately below the third trochanter, to the lateral surface of the lateral condyle, and to the capsule of the knee-joint at the side of the patella and patellar ligament.

*M. Gluteus medius*.—Rises from the lateral surface of the ilium and inserted into the summit and lateral aspect of the great trochanter, extending down to the level of the upper border of adductor magnus and almost down to the level of the insertion of gluteus maximus.

Text-figure 10.



Lateral aspect of thigh (left).

- |               |              |                  |                  |
|---------------|--------------|------------------|------------------|
| 1. Glut. max. | 16. Biceps.  | 23. Fem.-coccyg. | 33. Tenuissimus. |
| 2. Glut. med. | 18. Semimem. | 25. Caudotem.    |                  |

*M. Gluteus minimus*.—Adherent to and not readily separable from the overlying fibres of gluteus medius. Rises from the ilium deep and posterior to the origin of the preceding muscle, and is attached to the anterior surface of the great trochanter.

*M. Piriformis*.—Rises from the posterior part of the sacro-iliac symphysis, the anterior fibres being fused with the posterior fibres of gluteus medius. Inserted into the tip of the great trochanter in front of gluteus medius. This muscle is absent in all the *Lipotyphla* (Leche) though present in Lemurs.

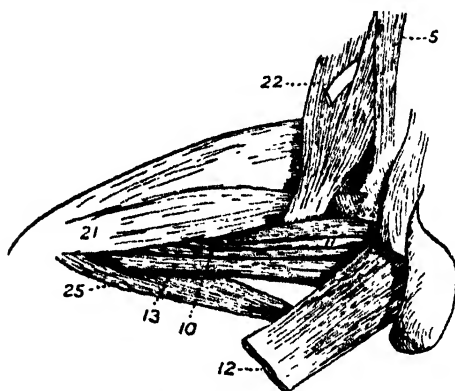
*M. Obturator internus*.—Rises from the whole circumference of the obturator foramen and the pelvic aspect of the obturator membrane. The tendon in the gluteal region is hidden by the gemellus muscle, with which it runs to the insertion at the posterior part of the great trochanter.

*M. Gemellus*.—This is a single muscle, the lower fibres being especially well-developed. It rises from the margins of the small sciatic notch, and is inserted with the obturator internus.

*M. Quadratus femoris*.—A triangular muscle rising from the lateral surface of the pubic arch, and inserted into the posterior aspect of the femoral shaft from the base of the great trochanter in a horizontal line extending towards the lesser trochanter.

*M. Caudofemoralis*.—Rises from the transverse processes of the 2nd and 3rd caudal vertebræ. The muscle divides into two parts, separated by the femoral vessels and enclosing between them the lower end of adductor magnus. The outer part is inserted into the lateral supracondylar ridge behind the upper

Text-figure 11.



Medial aspect of thigh (right).

5. Psoas minor.  
7. Pectineus.

10. Add. brev.  
11. Add. long.  
12. Gracilis.  
13. Add. mag.

21. Vastus int.  
22. Ilio-psoas.

(Other references as in text-fig. 10.)

fibres of femorococcygeus. The inner part gains an attachment to the medial epicondyle immediately medial to and above the origin of the inner head of gastrocnemius, and deep to the anterior fibres of semimembranosus.

Leche notes that the muscle is absent in the *Lipotyphla*. It is, however, present in the *Lemuroidea* and also in *Tarsius* (Appleton, 1).

*M. Tenuissimus*.—Rises from the aponeurosis covering the dorsal caudal muscles immediately behind gluteus medius. Crosses superficial to the great sciatic nerve and then deep to the biceps. Inserted into the fascia of the leg below and in continuity with the insertion of biceps, being overlapped slightly by the lower margin of the latter muscle.

This muscle is supplied by a branch from the common peroneal component of the sciatic nerve.

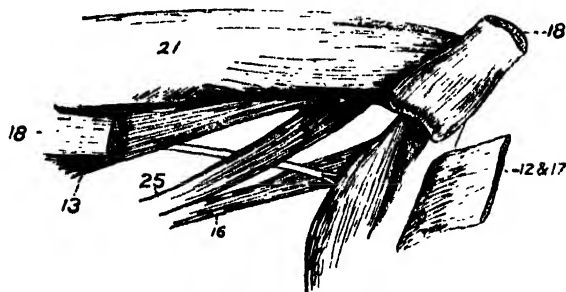
*M. Biceps*.—Rises from the ischial tuberosity, and is inserted by a broad fascial expansion into the upper half of the outer aspect of the leg as far forwards as the crest of the tibia and reaching up to the level of the lower border of the patella. It gains' indirect attachment only to the head of the fibula. The upper part of the muscle receives a twig from the tibial component, and the lower part a twig from the common peroneal component of the sciatic.

*M. Semitendinosus*.—This muscle has two heads of origin:—

- (1) From the 2nd and 3rd caudal vertebræ deep to caudo-femoralis.
- (2) From the ischial tuberosity.

These two laminæ fuse together fairly quickly below their origin to form a thick belly, which ends in a thin flattened

Text-figure 12.



Inner side of knee (left).

17. Semitendinosus.

(Other references as in text-figs. 10 and 11.)

tendon that gains insertion to the crest of the tibia deep to gracilis.

*M. Semimembranosus*.—Rises from the ischial tuberosity and posterior half of the lower border of the pubic arch. Inserted into the medial aspect of the medial tibial condyle close to the articular surface and immediately posterior to the internal lateral ligament, medial surface of the medial femoral condyle, and lower end of the medial supracondylar ridge.

*M. Sartorius*.—Rises from the inguinal ligament from a point superficial to the femoral vessels as far medially as the pubic spine, where the innermost fibres gain attachment. Inserted into the antero-medial surface of the tibia immediately medial to the tibial crest.

Leche notes that the sartorius is absent in all the Lipotyphla except *Erinaceus*.

*M. Gracilis*.—Rises from the whole length of the pubic arch. Inserted into the antero-medial surface of the tibia medial to the lower end of the tibial crest, the insertion being in continuity with that of sartorius.

*M. Pectineus*.—Rises from the surface of the pubis immediately lateral to the pubic spine, and is inserted into the upper end of the posterior surface of the femoral shaft. Its nerve-supply is derived from the ant. crural nerve.

*M. Adductor longus*.—Rises from the anterior third of the pubic arch immediately caudal to pectineus and anterior to the origin of adductor magnus. Inserted into the middle third of the shaft of the femur. This is a narrow muscle ending in a broad thin expansion at its insertion.

*M. Adductor brevis*.—A large thick muscle, rising from the pubis lateral to the symphysis and inserted into the shaft of the femur from the lower border of pectineus to the junction of the third and lower quarters of the femur.

*M. Adductor magnus*.—Rises from the middle third of the pubic ramus. No origin from the tuber ischii. Inserted into the posterior aspect of the shaft of the femur from the posterior surface of the third trochanter down to the popliteal surface. The lower fibres are pierced by the femoral vessels.

*M. Rectus femoris*.—Origin from the anterior inferior iliac spine and cephalic margin of the acetabulum. There is no clear distinction between the "straight" and "reflected" heads of human anatomy. Inserted into upper margin of patella.

*M. Obturator externus*.—Rises from lower and posterior margin of obturator foramen and from the outer surface of the obturator membrane. Inserted into the fossa on the posterior aspect of the great trochanter.

*M. Vastus lateralis*.—Rises from the anterior aspect of the great trochanter immediately below the insertion of gluteus minimus. No origin from the remainder of the femoral shaft. The muscle is accommodated in the groove which is present on the front of the third trochanter. Inserted into the lateral side of the common quadriceps tendon, and by a fascial expansion into the lateral margin of the patella.

*M. Vastus medialis*.—Rises from the anterior and medial aspects of the femoral shaft from a point 2 mm. below the level of the small trochanter up to the base of the great trochanter immediately below the origin of vastus lateralis. Inserted into the medial side of the common quadriceps tendon and medial patellar margin.

*M. Vastus intermedius*.—A small but distinct muscle, rising from the anterior, medial, and lateral aspects of the femoral shaft below, extending up the anterior surface as far as the level of the lower end of the small trochanter. Inserted into the upper margin of the patella. According to Leche, an independent crureus is only found in *Erinaceus* among the Lipotyphla, while

a subcrureus is not found in any insectivore. I agree that usually no differentiated subcrureus can be identified in *Tupaia*, but I have found one exception to this in a specimen of *T. minor*, in which there was a very distinct subcrureus rising from the anterior aspect of the femur, almost as far proximally as the middle of the shaft.

*M. Tibialis anticus*.—Rises from the upper half of the lateral surface of the tibia, from the upper third of the antero-medial aspect of the fibula, and from the fascia covering extensor longus hallucis, as well as from the interosseous membrane. Inserted into the internal cuneiform and the base of the first metatarsal.

*M. Extensor longus digitorum*.—Rises by a rounded tendon from the lateral aspect of the external condyle of the femur immediately in front of the femoral attachment of the long external lateral ligament. On the dorsum of the foot the tendon divides into four to supply the outer four digits, blending with the corresponding tendons of the extensor brevis and peronei to gain attachment to the middle and distal phalanges. In the origin of this muscle *Tupaia* agrees with the Lipotyphla and differs from the Lemurs. This origin, however, is probably to be regarded as primitive (Ribbing).

*M. Extensor longus hallucis*.—Origin from middle third of the fibula and interosseous membrane and slightly from the adjacent part of the tibia. The muscle forms a very fine tendon, which is bound down to the tibialis anticus tendon at the latter's insertion, and thence runs straight along the dorsum of the first metatarsal bone to the terminal phalanx, sending also a few fibres of attachment to the base of the proximal phalanx.

*M. Peroneus longus*.—Rises from the upper quarter of the lateral surface of the fibula. No origin from the femur or from the lateral ligaments of the knee-joint. The tendon winds round the lateral aspect of the cuboid, and at this point it is slightly thickened, but shows no indication of a sesamoid body. It is inserted into the lateral surface of the internal cuneiform and the base of the first metatarsal.

*M. Peroneus brevis*.—Rises from the lower two-thirds of the fibula, below from the lateral surface and above curling round on to the posterior surface. Inserted into the base of the fifth metatarsal.

*M. Peroneus quinti et quarti digiti*.—A perfectly distinct muscle, divided into two muscular bellies ending in very slender tendons. The upper part rises from the second quarter of the fibula behind the peroneus brevis and from intermuscular septa. The lower part takes origin from the middle third of the fibula. The upper part sends its tendon to the fifth digit, piercing and receiving a reinforcement from the tendon of peroneus brevis. The lower part runs to the 4th and 5th digits, mainly to the former.

The differentiation of this muscle into two distinct parts is paralleled by the condition found in Lemuroidea.

*M. Extensor brevis digitorum*.—Rises from the upper surface of the os calcis. It is divided into three muscular bellies and three main tendons. Of the latter, the innermost divides to supply the 1st and 2nd digits, and the other two pass to the 3rd and 4th digits. The tendon of the hallux blends with that of the extensor longus hallucis and gains insertion into the base of the terminal phalanx.

Dohson (3) noted one specimen of *Gymnura* in which the hallux received a very slender tendon from ext. brevis digitorum, but apart from this case, which he evidently regards as exceptional, in none of the Lipotyphla does the muscle contribute a tendon to the hallux. Herein the Tree-Shrew approximates to the Lemuroid condition and differs from the Insectivora.

*M. Popliteus*.—Rises from the femur immediately below the origin of the ext. longus digitorum. Inserted into the posterior aspect of the upper quarter of the tibial shaft.

Carlsson points out that in the comparatively small extent of its insertion this muscle resembles that of Lemurs rather than that of Insectivora or *Sciurus*.

*M. Flexor longus digitorum*.—Rises from the upper two-thirds of the posterior aspect of the tibia, the origin extending over the fascia covering popliteus and along the bone at the medial margin of the muscle to reach the head of the tibia above.

*M. Flexor longus hallucis*.—A large muscle, rising from the lateral margin of the posterior surface of the tibia as far up as the popliteus, from the interosseous membrane, and from the whole length of the fibula. Above, its origin extends on to the lateral surface of the fibula, the muscle passing down deep to soleus to reach the posterior surface.

The tibial origin of this muscle is variable, in some cases being confined to the lower third of the bone below the attachment of tibialis posticus.

*M. Tibialis posticus*.—A small muscle, rising from the intermuscular septa, gaining also a slight attachment to the posterior surface of the upper end of the fibula, medial to flexor longus hallucis. In some cases the origin extends on to the outer margin of the tibia between popliteus and flexor longus hallucis. Inserted into the navicular bone.

*M. Gastrocnemius*.—Rises by the usual two heads from the posterior aspect of the femur immediately above the articular condyles, the lateral attachment being blended with the origin of the plantaris. Osseous fabellæ are present in the two heads. Both bellies are equal in size, and form a tendon somewhat stouter than that of soleus. Inserted into the tuberosity of the calcaneum.

*M. Soleus*.—Rises from the postero-lateral aspect of the fibula, middle third, bridging across the flexor longus hallucis (whose fibres rise alongside the peroneus longus from the lateral aspect of the upper end of the fibula) to gain origin from the posterior surface of the head of the fibula.



*M. Plantaris*.—A well-developed muscle, fleshy down to within 4 mm. of the insertion of tendo achillis. Rises from the posterior aspect of the lateral condyle of the femur and partly from the fascia between it and gastrocnemius. The tendon passes round the calcaneal tuberosity to end in the plantar fascia.

*M. Flexor brevis digitorum*.—This is a complex muscle with a variety of origins forming four tendons which supply the outer four digits. That part which supplies the 5th digit rises entirely from the deep aspect of the plantar fascia. The components which supply the 3rd and 4th digits derive their origin from the medial part of the calcaneal tuberosity, from the surface of the deep flexor tendons, and, to a great extent, from the plantar fascia. The tendon to the 2nd digit is derived from a muscular belly, which rises almost entirely from the calcaneum

Text-figure 13.



Flexor brevis digitorum.

Text-figure 14.



Diagram illustrating the composition of Fl. brev. digit.

alone as a rule, though in one specimen of *T. minor* it also possessed a deep head, rising from the deep flexor tendons.

In possessing two heads of origin, from the deep flexor tendons and the plantar fascia, the flexor brevis digitorum of *Tupaia* conforms to the arrangement found in the Lemuroidea and differs from the Lipotyphla and *Sciurus*. In the direct attachment of the muscle to the os calcis, *Tupaia* appears to be paralleled only by the Primates and certain Chiroptera (Anthony & Vallois).

*M. Abductor hallucis*.—Rises from the inferior surface of the navicular lateral to the tubercle. Inserted into the medial side of the base of the proximal phalanx of the hallux. This muscle appears to be absent in the Lipotyphla (Dobson), though it is always found in the Lemuroidea.

*M. Flexor brevis hallucis*.—Origin from the base of the first metatarsal. Inserted into both sides of the base of the proximal phalanx, but mainly to the medial side.

*M. Abductor minimi digiti*.—Rises from the tuberosity of the calcaneum, and is inserted into the lateral side of the base of the proximal phalanx of the little toe.

*M. Abductor ossis metatarsi minimi digiti*.—Rises from the lateral side of the calcaneal tuberosity and lateral surface of the calcaneum, and is inserted into the outer side of the base of the fifth metatarsal.

*M. Accessorius*.—Rises mainly from the prominent tubercle situated at the anterior end of the infero-lateral margin of the calcaneum immediately anterior to the posterior tubercles. Inserted into the lateral and posterior margins of the bony plaque in the deep flexor tendons.

Text-figure 15.



Deep flexor tendons in sole of foot, with accessorius.

*M. Flexor brevis minimi digiti*.—Rises from the plantar surface of the shaft of the fifth metatarsal, and inserted into the base of the proximal phalanx.

*M. Contrahentes*.—These are three in number, and are related to the hallux, index, and minimus digits. They all rise from the fibrous sheath covering the tendon of peroneus longus.

*Deep flexor tendons*.—These unite in the sole to form a common mass, in which is developed a bony plaque. The latter is oval in shape, and penetrates through the whole thickness of the tendons. It is thus difficult or impossible to determine from which long flexor muscle each flexor tendon to the toes is derived. The tendon to the hallux appears to be mainly derived from the flexor tibialis.

*M. Lumbricales*.—These are four in number, and are disposed in the usual manner.

*M. flex. breves profundi*.—Including the short flexors of the

1st and 5th digits (already described), each toe possesses two flexors.

*M. Sterno-cleido-mastoideus*.—This muscle can be divided into three parts:—

- (1) Sterno-mastoid.
- (2) Cleido-mastoid.
- (3) Cleido-occipital.

There is no sterno-occipital component. The cleido-occipital, which lies superficial to the cleido-mastoid, rises from the occipital crest medialwards to a point midway between the mastoid and occipital protuberance. Inserted into the anterior and cephalic aspects of the inner end of the clavicle.

The spinal accessory nerve passes between the cleido-mastoid and cleido-occipital components, and deep to the sterno-mastoid portion.

*M. Sterno-hyoidens*.—A relatively broad band of muscle in close contact with its fellow of the opposite side in its whole extent. Rises from the posterior surface of the manubrium sterni (no clavicular attachment), and is inserted into the lower border of the body of the hyoid bone.

*M. Sterno-thyroideus*.—Lies deep to the preceding muscle and is narrower, meeting its fellow of the opposite side in the mid-line below at the cephalic end of the sternum. Rises from the back of the manubrium sterni and the cartilage of the first rib. Inserted into the lower margin of the lateral surface of the ala of the thyroid cartilage, reaching to within 2 mm. of the mid-line.

*M. Omohyoid*.—A flat muscle of uniform width, with an oblique and faintly-marked tendinous intersection in the middle of its course. Attached above to the lower border of the hyoid bone lateral to the sterno-hyoid, and below to the upper border of the scapula, close to the base of the coracoid process.

The presence of a distinct intersection in this muscle is of importance. Parsons states that it is only found in Primates and Chiroptera, while one may infer from Dobson that it is absent in the lipotyphlous insectivores. It has been found in all the specimens of *T. minor* and *T. ferruginea* examined.

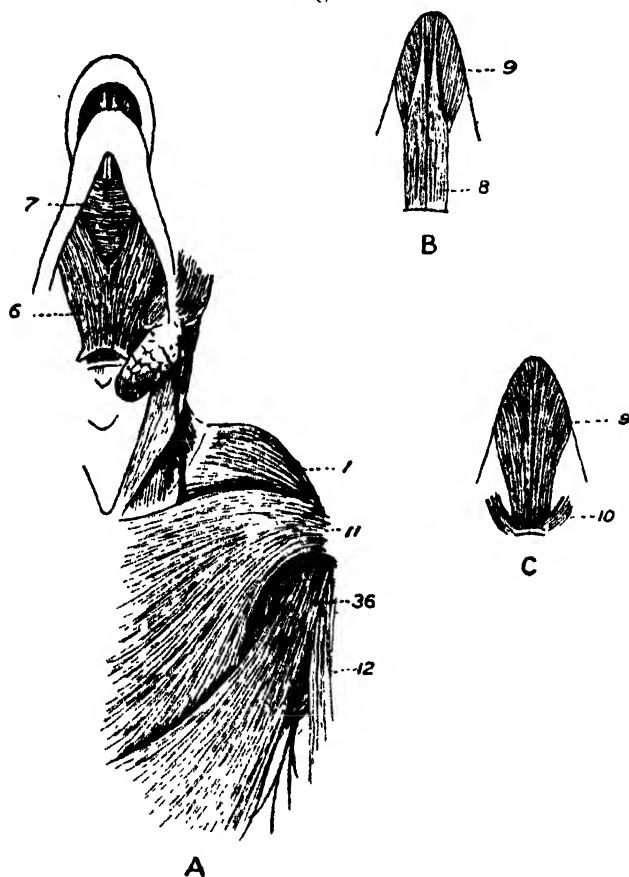
*M. Mylohyoideus*.—Rises from the mylohyoid ridge of the mandible, and is inserted into a median raphe, which extends from the body of the hyoid bone to a point 2 mm. behind the symphysis menti. The anterior 4 mm. of the muscle is fairly definitely separated from the posterior fibres by the entrance of the mylohyoid nerve into the muscle.

*M. Digastricus*.—The two bellies of this muscle are separated by a well-marked tendon, which unites with that of the opposite side to form an arch lying immediately anterior to the hyoid bone. The posterior belly rises from a depression at the postero-lateral margin of the bulla. The anterior belly rises from the anterior margin of the tendinous arch, and is inserted into the lower

margin of the mandible extending from the anterior margin of the masseter as far forwards as a point 4 mm. from the symphysis menti.

*M. Geniohyoideus*.—A narrow strip of muscle, rising from the body of the hyoid bone close to the mid-line and ending

Text-figure 16.



Muscles of submental region.

- |               |                     |                  |
|---------------|---------------------|------------------|
| 1. Deltoid.   | 8. Geniohyoid.      | 11. Pect. major. |
| 6. Digastric. | 9. Geniohyoglossus. | 12. Dorso-hum.   |
| 7. Mylohyoid. | 10. Hyoglossus.     | 36. Abd. hum.    |

anteriorly in a narrow flat tendon, which is inserted into the lower border of the mandible at the side of the symphysis menti.

*M. Geniohyoglossus*.—Rises from the upper margin of the body

of the hyoid bone. It forms a deep muscle, of which the upper fibres are inserted into the mucous membrane of the tongue, while the lower gain attachment to the inferior margin of the mandible extending from the symphysis backwards for 3 or 4 mm.

*M. Hyoglossus*.—Rises from the great cornu and body of the hyoid superficial to geniohyoglossus, its origin extending to the mid-line. The fibres run upwards and forwards to the side of the tongue.

*M. Thyrohyoideus*.—Rises from the ala of the thyroid cartilage close to its lower border, and is inserted into the great cornu of the hyoid bone.

*M. Stylohyoideus*.—Rises from the whole length of the anterior aspect of the stylo-hyal. The muscle runs alongside the mandibular ramus deep to the mandibular attachment of geniohyoglossus.

*M. Temporalis*.—This muscle may be divided into three parts:—

- (a) Superficial head—which rises from the anterior half of the temporal crest and the aponeurosis covering the deep part of the muscle. The fibres run mainly downwards and forwards, passing superficial to the zygomatic head to gain insertion to the anterior margin of the coronoid process.
- (b) Deep head—rising from the posterior half of the temporal ridge and from the whole extent of the temporal fossa. Inserted into the anterior and posterior margins of the tip of the coronoid process.

The lowermost fibres are blended indistinctly with those of the external pterygoid, and gain insertion to the upper part of the deep surface of the coronoid process and ascending ramus. This head is covered by a well-marked glistening aponeurosis, which gives origin to fibres of both the superficial and deep head.

- (c) Zygomatic head—rising from the upper border of the zygomatic arch and partly from the deep surface. The fibres arch forwards to gain attachment to the outer surface of the coronoid process.

The remarkable resemblance of this muscle to the temporalis of *Tarsius* is noteworthy.

*M. Masseter*.—This muscle can without much difficulty be divided into superficial and deep layers, especially in young specimens. In the latter the superficial fibres rise from the anterior half of the lower border of the zygomatic arch, while the deep fibres rise from the posterior half of the lower border and the whole of the deep surface. In adult animals the distinction between superficial and deep layers at their origin is not so clear. The superficial fibres gain attachment to the angle of the jaw, extending along the lower border of the mandible to blend anteriorly with the internal pterygoid. The deep fibres run more

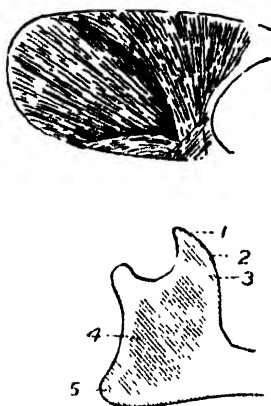
vertically downwards to gain insertion into the greater part of the lateral surface of the ascending ramus.

*M. Pterygoideus externus*.—A feebly-developed muscle which rises from the lateral aspect of the lateral pterygoid plate and inferior aspect of the tympanic bulla.

*M. Pterygoideus internus*.—A well-developed muscle, rising from the ectopterygoid fossa and gaining insertion to the medial aspect of the angle of the mandible. This muscle is not well differentiated from the preceding muscle.

*M. Quadratus lumborum*.—A somewhat slender muscle, rising from the medial end of the lower border of the last rib and the transverse processes of all the lumbar vertebræ. Inserted into the crest of the ilium, extending laterally to within 2 mm. of the anterior superior spine.

Text-figure 17.



Temporal muscle and muscle attachments to ascending ramus of mandible (left).

- |                  |                |              |               |
|------------------|----------------|--------------|---------------|
| 1. Temp. muscle. | Deep head.     | 4. Masseter. | Deep head.    |
| 2. " "           | Superf. head.  | 5. " "       | Superf. head. |
| 3. " "           | Zygomat. head. |              |               |

*M. Diaphragm*.—This muscle is roughly circular, with a transverse diameter of about 18 mm. and a sagittal diameter of a little over 20 mm. It is attached to the costal cartilages of the lower ribs, the xiphisternum, and the bodies of the upper four lumbar vertebræ. The crus of the diaphragm is formed by the union of the two margins of the elongated œsophageal opening, forming a tendon with a sharp anterior border which is attached to the bodies of the lumbar vertebræ slightly to the right of the mid-line. The aorta pierces the muscular part of the diaphragm on the left side of the crus, the muscle fibres on the lateral side of the aorta passing behind the vessel to be inserted into the crus.

The central tendon can be divided into three lobes, of which the central is large and rounded, while the lateral are narrow and

tapering. The caval opening lies at the anterior margin of the junction of the right and central lobes. The dimensions of the tendinous lobes are as follows :—

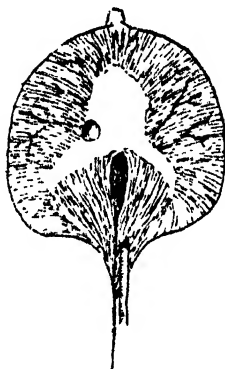
	Sagittal.	Transverse.
Anterior.....	7·5 mm.	5·5 mm.
Right .....	7·5 „	2·5 „
Left .....	8 „	1·5 „

The dome of the diaphragm extends up to the level of the 8th or 9th thoracic vertebra.

*M. Psoas major*.—Rises from the bodies of the 4th to 7th lumbar vertebrae inclusively. Inserted into the small trochanter.

*M. Psoas minor*.—Origin from first three lumbar vertebrae and the upper border of the fourth. Inserted into the ilio-pectineal line.

Text-figure 18.



Abdominal surface of diaphragm.

*M. Iliacus*.—This muscle may be described as consisting of two parts—a medial and lateral. The medial portion rises from the upper five lumbar vertebrae. Its tendon of insertion remains separable from the adjoining muscles, and is attached to the femur immediately below the small trochanter. The lateral portion rises from the whole of the iliac fossa, and blends with the psoas major to gain insertion into the small trochanter.

Leche has drawn attention to the resemblance between the iliacus muscles of *Tupaia* and *Galago*. I have confirmed this by a dissection of *Galago*, and I may add that the muscle is disposed in the same manner in *Tarsius*.

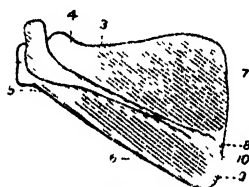
*M. Erector spinæ*.—This muscle mass may be conveniently divided into three columns:—

1. The outer column rises from the crest and the posterior part of the mesial surface of the ilium, from the posterior aspect

of the sacro-iliac symphysis and adjacent part of the sacrum, and from the lumbar fascia. It is partly inserted into the transverse processes of the lumbar vertebrae, and above it divides into two subsidiary columns. Of these the lateral is a slender column, gaining attachment to the angles of the lower ribs, more fibres rising mesial to the insertions to run to the upper ribs and the transverse processes of the last two or three cervical vertebrae. The mesial, a more bulky mass, is inserted laterally into the lower ribs and medially into the transverse processes of the thoracic vertebrae. More fasciculi rise from the transverse processes of the lower thoracic vertebrae by a tendinous origin, and run to the upper ribs and the transverse processes of the 2nd to 5th cervical vertebrae inclusively. A few of these upper fibres run medially to be inserted into the first two or three dorsal vertebrae and the last one or two cervical vertebrae, becoming continuous thus with *semispinalis colli*.

2. The middle column rises from the transverse processes of all the lumbar and sacral vertebrae, and runs downwards to form seven or eight long fine tendons, which pass down the dorsum of

Text-figure 19.



Muscle attachments to scapula (left).

1. Deltoid. 2. Lev. scap. 4. Trapezius. 5. Triceps (long head).  
(Other references as in text-fig. 3.)

the tail, being joined below by further fasciculi that rise from the caudal vertebrae.

3. The inner column forms a large fleshy multifidus spinæ, running between the transverse and spinous processes of the lumbar and lower thoracic vertebrae. *Semispinalis dorsi* is a well-defined muscle lying superficial to the upper end of the middle column, rising from the lower dorsal transverse processes and being inserted into the upper dorsal spines.

*M. Semispinalis colli*.—The upper fibres of this muscle run to the transverse process of the atlas, and do not converge on to the spinous process of the axis. A small bundle of fibres rises in the same plane from the sides of the upper two or three dorsal spines to run to the transverse process of the atlas. A few fibres also, rising from the upper two dorsal spines and the lower cervical vertebrae, pass to the upper cervical spines, ending at the spinous process of the axis above.



*M. Rectus capitis posticus major*.—Rises from the spine of the axis, and is inserted into the occipital bone beneath complexus.

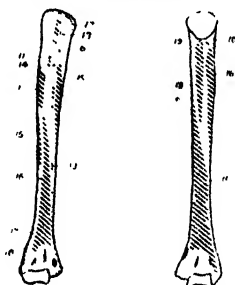
*M. Obliquus superior*.—Rises from the transverse process of the atlas. Inserted into the occipital bone deep to complexus, and overlapping the insertion of the preceding muscle.

*M. Obliquus inferior*.—Runs from the spinous process of the axis to the transverse process of the atlas.

*M. Rectus capitis posticus minor*.—Origin from the posterior tubercle of the atlas; insertion into the posterior margin of the foramen magnum. All these suboccipital muscles are well-developed.

*M. Splenius capitis*.—Rises from the median nuchal raphe and the first dorsal spine. The muscle extends to the mid-line up to its insertion into the skull from the occipital protuberance to the mastoid.

Text-figure 20.



Muscle attachments to humerus (right).

6. *Teres major*.      12. *Dorso hum.*      18. *Ext. c. rad. long.*

(Other references as in text-figs. 6 and 7.)

*M. Splenius colli*.—No representative of this muscle is present.

*M. Semispinalis capitis*.—Rises from the lower four cervical and the upper seven dorsal vertebræ. Inserted into the occipital bone below the occipital crest. The outer part of the muscle has a very fine transverse intramuscular septum.

*M. Serratus posticus*.—This is a continuous sheet of muscle attached to all except the first two ribs.

The *Serratus posticus superior* rises deep to *rhomboides* from the nuchal raphe and the first three dorsal spines. The fibres run downwards and outwards to the 3rd to 10th ribs inclusively.

The *Serratus posticus inferior* rises from the last seven dorsal spines and is attached to the lower five ribs, the fibres running outwards and a little upwards. At the 9th and 10th ribs the superior and inferior sheets overlap, the fibres of the former passing deep to those of the latter.

*M. Longissimus capitis*.—Rises from the transverse processes

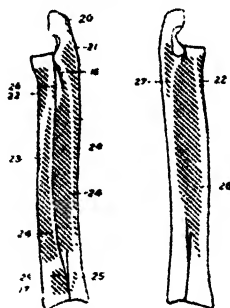
of the 2nd to 5th cervical vertebræ, and is inserted into the mastoid process.

*M. Rectus capitis anticus major*.—Rises from the transverse processes of the 5th, 6th, and 7th cervical vertebræ. Inserted into the basi-occipital bone.

*M. Rectus capitis anticus minor*.—Origin from the transverse process of the atlas. Insertion into the basi-occipital bone posterior to the preceding muscle.

*M. Longus colli*.—The upper oblique part of this muscle consists of two parts: (a) rising from transverse processes of C 3, 4, and 5, and inserted into the front of the atlas close to the mid-line; and (b) rising from transverse processes of C 5 and 6, and inserted into the front of the axis. The lower oblique portion rises from the bodies of the first five dorsal vertebræ, and is inserted into the transverse processes of the last two cervical vertebræ.

Text-figure 21.



Muscle attachments to radius and ulna (right).

20. Condylo-olecran. 21. Fl. carp. uln. 24. Fl. profundus. 25. Pron. quad.  
(Other references as in text-figs. 6, 7, and 8.)

The vertical part of longus colli runs between the first three dorsal vertebræ below and the last five cervical vertebræ above.

*M. Scalenus anticus*.—Rises from the transverse processes of all the cervical vertebræ, with the exception of the last. The muscle runs down to the first rib, passing between the subclavian vein and artery.

*M. Scalenus medius*.—Rises from the transverse processes of the 4th and 5th cervical vertebræ, and is inserted into the first rib behind the subclavian artery.

*M. Scalenus posticus*.—Rises from the transverse processes of all but the last cervical vertebræ, and is inserted into the 2nd to 5th ribs, the medial margin of the muscle lying in contiguity with the lateral margin of the rectus abdominis.

*M. Serratus anticus*.—Rises from the transverse processes of all the cervical vertebræ and from the upper nine ribs. Inserted into the lower half of the vertebral border of the scapula, the lower five digitations being concentrated on the inferior angle.

*M. Rectus abdominis*.—A continuous band of muscle, rising from the length of the pubic crest by a simple linear origin and extending laterally slightly behind the pubic spine. Inserted into the whole length of the front of the first rib and to the sternal ends of the 2nd, 3rd, and 4th costal cartilages. No tendinous intersections can be detected in the muscle. In *T. ferruginea*, however, the intersections are well-marked and five in number. The most posterior intersection traverses the muscle at the middle of its abdominal course, and the most anterior at a distance of 12 mm. above the xiphisternal junction. The remaining three are disposed at more or less regular intervals between these two.

Leche did not find these intersections in *T. ferruginea*, and Kaudern also states that they are absent in *T. javanica*.

Text-figure 22.



Muscle attachments to Os Innominatum (left).

- |               |               |                      |
|---------------|---------------|----------------------|
| 3. Glut. min. | 8. Ext. chl.  | 14. Ischiococcygeus. |
| 4. Rect. fem. | 9. Add. long. | 15. Gemellus.        |
| 6. Sartorius. | 11. Obt. ext. | 19. Quad. fem.       |

(Other references as in text-figs. 10, 11, and 12.)

*M. Pyramidalis* well-developed. Rises from the whole length of the pubic crest, and is inserted into the linea alba upwards for about 13 mm.

*M. Triangularis sterni*.—Rises from the margin of the xiphisternum and the body of the sternum, and is inserted into the 2nd and 7th costal cartilages. This muscle continues uninterruptedly the series of costal attachments of the transversalis muscle.

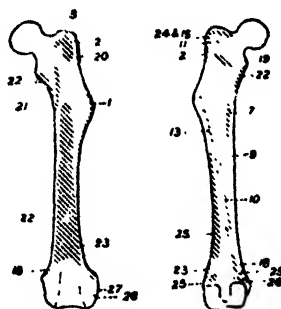
*M. Obliquus externus*.—Rises by a series of digitations from the lower nine ribs and from the lumbo-dorsal fascia. The muscle is inserted into the cephalic extremity of the ilium, to the inguinal ligament, to the anterior end of the symphysis pubis, the anterior margin of the pubis as far laterally as the pubic spine, and into the linea alba. At the latter insertion the muscle remains fleshy almost to the mid-line. In the male the lower insertion of the

muscle is divided into two distinct bands, between which pass out the spermatic cord and the cremaster muscle.

In *T. ferruginea* (as first pointed out by Leche) this muscle on its lateral aspect shows a series of four or five well-marked tendinous inscriptions which run medially and caudalwards, cutting obliquely across the more caudally-directed fibres of the muscle. These tendinous inscriptions cannot be detected in *T. minor*.

*M. Obliquus internus*.—Rises from the lumbo-dorsal fascia and the whole length of the inguinal ligament, reaching on to the tip of the ilium. Inserted into the sheath of the rectus at the outer border of this muscle, and into the lower three costal cartilages. The anterior part of this muscle is considerably thinned out, the fibres diverging to expose the underlying transversalis muscle. The insertion of the internal oblique contributes to the formation of the posterior layer of the rectus sheath in the anterior half of

Text-figure 23.



Muscle attachments to femur (left).

- |               |                |                       |                    |
|---------------|----------------|-----------------------|--------------------|
| 3. Glut. min. | 15. Gemellus.  | 21. Vast. int.        | 26. Gastroc.       |
| 9. Add. long. | 19. Quad. fem. | 22. Crureus and ilio- | 27. Ext. l. digit. |
| 11. Obt. ext. | 20. Vast. ext. | psaos.                | 28. Popliteus.     |

(Other references as in text-figs. 10 and 11.)

the extent of the latter muscle, and to the anterior layer in the posterior half. In the male the most caudal fibres contributed to the formation of the cremaster muscle.

Kaudern (5) points out that in no other insectivore does the internal oblique possess this method of insertion into the rectus sheath, and that, with the exception of the *Talpinae*, the muscle in the *Insectivora* passes ventral to the rectus. In this connection *Tupaia* is associated with the Lemurs.

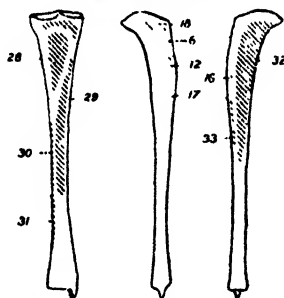
*M. Transversalis*.—Rises from the lower six costal cartilages, the lumbo-dorsal fascia, and the whole length of the inguinal ligament. The anterior part of the muscle is well-developed, forming a relatively thick layer, which passes to the side of the xiphisternum in front of the caudal extremity of the origin of

pectoralis major and behind the anterior half of the rectus to the linea alba. The posterior part of the muscle is thinner, and not easily separable from the overlying internal oblique. With the latter muscle the transversalis ends in a fascial expansion, which contributes to the formation of the anterior layer of the rectus sheath over the posterior half of the extent of the rectus muscle. The most caudal fibres of the muscle appear to assist in the formation of the cremaster muscle in the male.

*M. Iliococcygeus*.—Rises from the ilio-pectineal line cephalad to the obturator foramen by a short fleshy origin. Inserted into the mid-ventral line of the base of the tail over the 2nd and 3rd caudal vertebræ.

*M. Pubococcygeus*.—This muscle has a more extensive origin than the preceding muscle, from which it is separated by the obturator nerve. It rises from the whole length of the deep surface of the cephalic ramus of the pubis as well as from the dorsal aspect of the pubic symphysis. Inserted into the hypopophyses between the 2nd and 3rd caudal vertebræ, its fibres overlapping medially those of the iliococcygeus.

Text-figure 24.



Muscle attachments to tibia (left).

- |                |                   |                   |
|----------------|-------------------|-------------------|
| 6. Sartorius.  | 29. Fl. l. digit. | 31. Ext. l. hall. |
| 28. Popliteus. | 30. Tib. post.    | 32. Tib. ant.     |

(Other references as in text-figs. 10, 11, and 12.)

*M. Ischiococcygeus*.—Rises from the dorsal margin of the ischium anterior to the ischial spine. Inserted into the transverse processes of the last sacral and the first three caudal vertebræ.

*M. Sacrococcygeus*.—A well-developed fleshy muscle, which takes origin from the lateral surface of the last two lumbar vertebræ, all the sacral, and the first two or three caudal vertebræ. The muscle is divisible into two distinct parts—a medial and lateral. Its forms posteriorly long slender tendons, which run along the ventral aspect of the tail to be attached to the hypopophyses and the lateral surfaces of the caudal vertebræ.

## DISCUSSION.

In the preceding description of the musculature of *Tupaia*, attention has been drawn to the various points in which the animal approaches or departs from Insectivora or Lemuroidea. If these are analysed in the following way, conclusions can be more readily drawn regarding the affinities of the Tree-Shrew.

A. The following conditions are found in *Tupaia*, and constitute the normal arrangement in Prosimiæ, while they are completely absent in the lipotyphlous Insectivora:—

1. M. Piriformis present.
2. M. Caudofemoralis present.
3. M. Brachioradialis present.
4. Double lateral head of triceps.
5. M. Obliquus internus passes, at its insertion anteriorly, dorsal to the rectus abdominis, whilst posteriorly it passes ventral to the muscle.
6. Comparative differentiation of the elements of Quadriceps extensor at their insertion.
7. Insertion of Popliteus not extending down further than the upper quarter of the tibial shaft.
8. Origin of Flexor brevis digitorum pedis.
9. Tendon to hallux derived from Extensor brevis digitorum.
10. Tendinous intersection in omohyoid.
11. Differentiation of M. Peron. quarti digiti.
12. Occasional distinct subcrureus.
13. Differentiation of the elements of ilio-psoas at their insertion.
14. Abductor hallucis present.

In addition to the above points *Tupaia* agrees with representatives of the Prosimiæ and departs from the Insectivora as follows:—

1. In the form of its temporal muscle, *Tupaia* agrees precisely with *Tursius*.
2. The form and disposition of M. Iliacus in *Tupaia* is identical with that found in *Galago*.

B. The following conditions are frequently absent among the Lipotyphla, though found in *Tupaia* and the Lemuroidea:—

1. Teres minor present.
2. Sartorius present.
3. Crureus differentiated.
4. Coracobrachialis fully developed.
5. Differentiation of Scalene muscles, with presence of Scalenus anticus.
6. Coracoid head of biceps present.
7. Differentiation of Flexor brevis pollicis and Flexor brevis minimi digiti.

In no single lipotyphlous insectivore is this group of muscles present as a whole, and yet it is found in its entirety in most members of the Lemuroidea.

C. In the following points *Tupaia* agrees with Lipotyphla and departs from the lemurine structure:—

1. Origin of Ext. longus digitorum from the femur.
2. Tenuissimus present.
3. Pyramidalis present.
4. Accessorius present.
5. Undifferentiated opponens muscles of the pollex and minimus digits.

A brief survey of this list shows them to be essentially primitive characteristics, and they therefore do not bear the usual significance in the matter of taxonomic value. The pyramidalis and accessorius muscles are found in the higher primates, while the tenuissimus is represented among these forms by the short head of biceps.

D. The following conditions appear to be peculiar to *Tupaia*:—

1. M. Spino-humeralis.
2. Double dorso-epitrochlearis.

Of these, the former is a differentiation of the cephalic fibres of latissimus dorsi, and is readily understood when it is noted that in many mammals there is a partial fusion of the latissimus dorsi with the teres major. The latter is a further elaboration of the common dorso-epitrochlearis muscle, for which it is difficult to find any adequate reason.

It is fully realized that the affinities of no animal (whose position is in any way obscure) can be estimated from a study of one anatomical system alone, and for this reason no certain conclusion can be drawn from the foregoing data. It is clear, however, that *Tupaia*, in its musculature, shows very remarkable resemblances to the Prosimiæ and corresponding differences from the lipotyphlous Insectivora, and were a systematist compelled in this case to rely entirely on comparative myology, there is little doubt that *Tupaia* would be approximated to the former and separated from the latter order.

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20. On some points in the Structure of the Pareiasaurian Skull\*. By R. BROOM, M.D., F.R.S., C.M.Z.S.

[Received April 1, 1924: Read May 6th, 1924.]

(Text-figures 1-6.)

Though *Pareiasaurus* was discovered by Andrew Bain in 1838, it was first described by Owen only in 1876. Since then many skulls and skeletons have been found; and Seeley has given full descriptions of the skeletons in the British Museum. In 1903 I described a good skeleton in the South African Museum, Cape-town; and in more recent years further light has been thrown on the structure by Watson, Haughton, and myself.

All this work has resulted in the postcranial skeleton being nearly fully known, and in the skull being fairly well known. There are, however, a good many points on which our knowledge is imperfect or lacking. Fossil reptiles got in the shales of the *Endothiodon* or *Cistecephalus* zones can be cleaned of matrix almost as perfectly as the skull of a recent animal, but most of the *Pareiasaurus* specimens come from the lower beds, where the matrix, unless weathered, is almost flinty hard, and the preparation of a *Pareiasaurus* skull is a matter usually of extreme difficulty. Further, the peculiar sculpturing of the cranial bones makes it in most cases almost impossible to trace the sutures. Occasionally specimens are discovered which are weathered in such a way that details of structure can be made out that are in most cases obscured.

*External Cranial Bones.*

Seeley in 1888 and 1892 first attempted to distinguish the cranial elements, but he was only partly successful. In the three skulls which I have described I found it impossible to trace the sutures on the outer surface. Where the roofing bones can be removed and their inner aspects examined, the sutures can be seen satisfactorily, and Watson in 1914 was able by this means to give a very good account of the various elements.

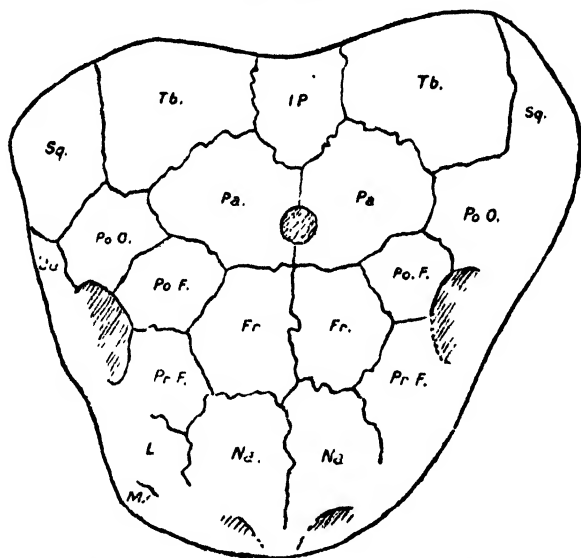
Mr. W. van der Byl, of Abraham's Kraal, has in his possession the skull of a young *Pareiasaurus* only a little more than half the adult size, and with the surface beautifully weathered. In this specimen almost all the sutures can be clearly seen. From

\* [Owing to an oversight, the total amount of reduction of the text-figures illustrating Dr. Broom's communication "On the Structure of the Skull in the Carnivorous Dinocerphalian Reptiles," published in Part IV. of the Society's Proceedings for 1923, was omitted. The correct figures should read as follows:—Figs. 1, 2, 4, 5, 6, 8, and 10, each about  $\frac{1}{2}$  nat. size; Figs. 3 and 12, each about  $\frac{1}{4}$  nat. size; Fig. 7, about  $\frac{1}{4}$  nat. size; Figs. 9 and 10, each about  $\frac{1}{4}$  nat. size.—EDITOR.]

the figure I give it will be seen that except in two points there is a close agreement with the sutures as revealed by Watson.

The nasals, frontals, and parietals form a series of three pairs of subequal bones, the parietals being only a little larger than the others. Above and behind the orbit lie three subequal bones—the prefrontal, the postfrontal, and the postorbital. Watson shows the postfrontal as a small bone wedged in between the other two. In my specimen the postfrontal is as large as the prefrontal. Watson's specimen is certainly a different species, and this may account for the difference, or, it may be, that when viewed on the inner aspect it appears smaller.

Text-figure 1.



Upper view of skull of young *Pareiasaurus* sp. About  $\frac{1}{2}$  nat. size. The skull is somewhat crushed from above downwards, and slightly distorted. Only those sutures are drawn which are clearly seen in the actual specimen.

Behind the parietals is a median unpaired interparietal. Watson believes there are two interparietals. In the specimen I have examined there is certainly only a single median bone. Outside the interparietal and behind the parietals are a pair of tabulars considerably larger relatively than in Watson's specimen. And outside of each tabular is a large squamosal. Below each squamosal is a large quadrato-jugal, not shown in the figure I give, as, owing to flattening of the skull by crushing, the quadrato-jugals pass down vertically and are not seen when the skull is viewed from above. In text-fig. 2 the quadrato-jugal is seen, as

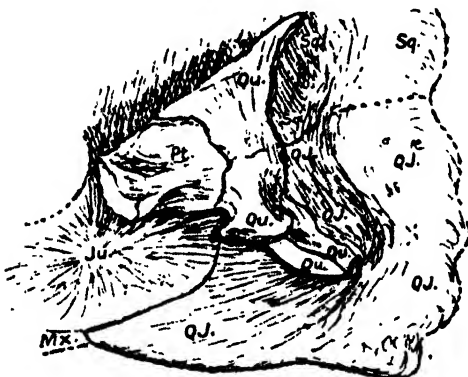
viewed from the inside, with the jugal and squamosal above it. The posterior end of the maxilla appears to meet the quadrato-jugal, as Watson shows. Unfortunately in the specimen figured in text-fig. 2 the maxilla is imperfect.

The lacrymal passes from the nostril to the orbit.

The determination of the species of any specimen of *Pareiasaurus* is at present a very hopeless business, and it is probable that the difficulty will long remain.

The type-specimen of *Pareiasaurus serridens* consisted of a fairly good skull, much crushed, and a large series of other bones. Owen apparently examined the original skull and had a plaster cast made of it. Unfortunately this type-skull is lost, and we have only the cast and a portion of the mandible left. Recently, however, Watson discovered in the British Museum quite a

Text-figure 2.



Quadrate and quadrato-jugal and their related bones viewed from the inside, of *Pareiasaurus* (*Bradysaurus*) *bombidens* Owen. About  $\frac{1}{2}$  nat. size.

number of postcranial skeletal elements which pretty certainly belong to the original type-animal. If these bones are correctly identified as belonging to the "Blinkwater monster," which became the type of *Pareiasaurus serridens*, then all the other known specimens which have been referred to *Pareiasaurus* (*Pareiasaurus bairi* Seeley, *Pareiasaurus bombidens* Owen, etc.) must belong to another genus or genera; for the bones unearthed by Watson show the presence of large numbers of bony scutes on the sides as well as the back—a character never met with in the Lower Beaufort *Pareiasaurs*. The classical specimen described by Seeley as *Pareiasaurus bairi*, Watson would call *Bradysaurus bairi*, and Owen's *Pareiasaurus bombidens* would also apparently become *Bradysaurus bombidens*. There is little doubt Watson is right in this matter of nomenclature, but how far the scientific

and general public will be inclined to reserve the name *Pareiasaurus* for a very imperfectly-known type, and to call the famous specimen which for years has been figured in text-books as *Pareiasaurus* by the new name *Bradysaurus* remains to be seen. In the meantime it will be a matter of convenience to consider the condition of the dermal scutes as merely a subgeneric character, and to call the Lower Beaufort forms *Pareiasaurus* (*Bradysaurus*) *bombidens* and *Pareiasaurus* (*Bradysaurus*) *baini*.

Only a few of the Lower Beaufort types are well preserved, and it will probably be years before we can have a satisfactory knowledge of *Pareiasaurus* systematically. Gradually it will improve. Thus the jaws and quadrate which I am describing in this paper are from Jan Willem's fontein—the same locality as yielded the type of *Pareiasaurus bombidens*, and I think it is moderately certain that this specimen belongs to Owen's species. Unfortunately, though my specimen reveals most of the skull structure, it gives no information as to the condition of the dermal scutes. There seems to be evidence of two species of *Pareiasaurus* in this same horizon of these lower beds. One has certainly three rows of small scutes in the vertebral region, but whether this species is *P. bombidens* remains unknown.

#### *The Quadrate and Quadrato-jugal.*

From the specimens which I have been studying it might be possible to give an account of most of the internal structure of the skull. But those specimens in which the brain-case is preserved in a tractable matrix are considerably crushed; while those which are uncrushed have a flinty matrix. I therefore think it better to leave a detailed description of the brain-case and ear region for the present, in the hope of shortly getting a specimen which may enable me to give good drawings of the structures.

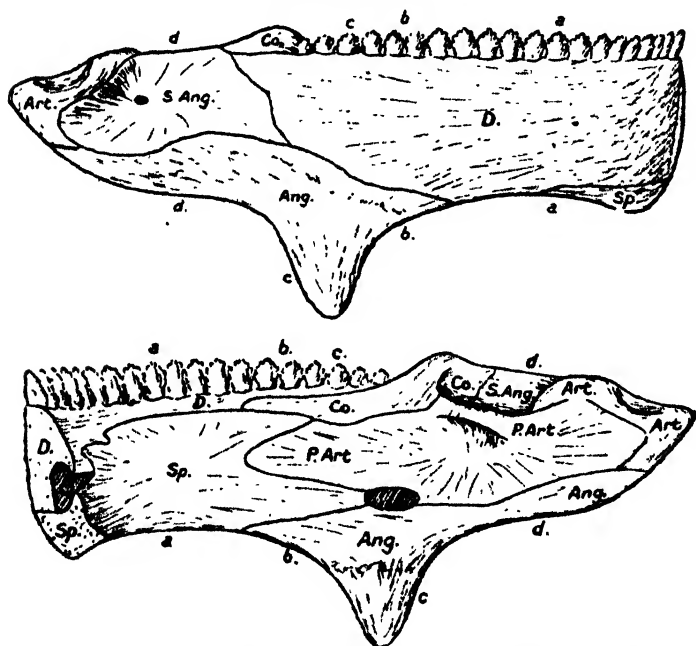
In one well-weathered skull the right quadrate and quadrato-jugal are almost perfectly preserved, and their relations with the neighbouring bones can for the most part be clearly made out.

The quadrato-jugal is a large bone which forms the lower and posterior part of the huge bony "cheek." The anterior half of the bone is moderately flat and thin; but the posterior portion is thickened into rounded bosses, which form the posterior border of the lateral part of the skull. Near the middle of the bone a stout anteriorly-directed ridge springs from the upper part, and firmly articulated to this is the lower part of the quadrate, as shown in the figure given. All that remains of the large opening usually present in reptiles between the quadrate and quadrato-jugal is a small foramen near the upper part of the quadrato-jugal. The anterior part of the quadrato-jugal gives a long articulation to the jugal, and appears to just meet the maxilla.

The upper part of the quadrato-jugal has a very broad articulation with the squamosal, where, owing to the great thickening of the bone, the suture is largely obscured.

The quadrate is a powerful bone, immovably articulated with the quadrato-jugal below and the squamosal above. The articular surface for the mandible is made up of an inner rounded face and an outer elongated oval face, with a shallow groove between them. Though this articular end is broad, the quadrate immediately above is much narrowed, and then, on passing upward, the bone again widens out to a broad flattened crest. This upper part is

Text-figure 3.



Mandible of *Pareiasaurus* (*Bradysaurus*) *bombidens* Owen.  $\frac{1}{4}$  nat. size.

Ang. Angular; Art. Articular; Co. Coronoid; D. Dentary; P. Art. Pre-Articular (Goniale); Sp. Splénial; S. Ang. Sur-Angular.

firmly clasped by an anteriorly deviated fold of the squamosal. The upper part of the quadrate has a flattened facet which probably gives articulation to the paroccipital, but which is lost in this specimen. Anteriorly the quadrate is closely and immovably articulated with the posterior process of the pterygoid. This posterior part of the pterygoid has a deep groove in which the anterior part of the quadrate rests. On the inner side the quadrate is completely covered at this part by the pterygoid, but

on the external surface the quadrate is seen passing forwards almost as far as the anterior end of the detached portion of the pterygoid seen in the figure.

In general structure the quadrate is not unlike that of *Sphenodon*, differing mainly in the fact that in *Pareiasaurus* the quadrato-jugal is enormous, and in *Sphenodon* almost rudimentary; but the relations of the anterior part of the quadrate to the pterygoid are remarkably *Sphenodon*-like.

### *The Mandible.*

The mandible has been described by Seeley as far as its general shape and characters are concerned, but without his being able to reveal much of its structure. He rightly, however, identified the large lower horn-like process as being formed by the angular. Watson in 1912 gave a much fuller account of the structure of the jaw, and endeavoured to determine the limits of the various elements with fair success. All the elements he has correctly identified, but in a good many points he is in error as to their limits. As very few jaws of Anapsid reptiles are at all fully known, a full knowledge of the jaw of *Pareiasaurus* will be of much service to future workers for comparisons.

The dentary is a large bone which forms considerably more than half of the outer surface of the jaw. In *Pareiasaurus* (*Bradysaurus*) *hombidens* Owen it carries twenty teeth. There is a deep powerful symphysis, with bones of the two sides firmly ankylosed. The lower third of the front jaw is formed by the splenial. Posteriorly the dentary articulates, as shown in the figure, with the surangular above and the angular below. Internally the dentary is seen to be largely concealed by the splenial and by the coronoid.

The splenial forms most of the inner side of the anterior half of the jaw, and the whole of the lower border of the anterior third. Its upper part overlaps much of the inner side of the dentary. Posteriorly it has a large articulation with the angular, and meets the prearticular and the coronoid, both of which it overlaps.

The coronoid is a small bone which forms a small coronoid process and the front of the upper opening into the cavity of the jaw. Its anterior portion rests on the dentary and articulates with the prearticular. Posteriorly the coronoid has an articulation with the surangular on the outer side of the opening into the jaw.

The prearticular is a large bone which forms about a third of the whole inner side of the jaw. Posteriorly it lies on the articular, to which it is closely attached. Inferiorly it articulates with the angular and the splenial, except at the place where there is the large foramen. Above, it forms the whole of the outer border of the upper opening into the jaw, and the anterior portion of the upper border of the bone articulates with the

coronoid. Watson has misunderstood the structure in this region, representing the coronoid as forming the lower and inner border of the upper opening. The sutures in this region are as I have shown them in the figure. The portion of the prearticular which forms the border of the upper opening is developed into a peculiar scroll-like structure which overhangs a deep hollow, but there is apparently no foramen here into the jaw.

The angular is a long bone which forms about two thirds of the lower border of the jaw and about a quarter of the outer surface of the jaw articulating above with the dentary and the surangular. Internally it articulates with the splenial and the prearticular, and posteriorly with the articular. The large horn-like process which passes down from the jaw is entirely formed by the angular. A large oval foramen is situated on the inside of the jaw between the splenial, the prearticular, and the angular.

The surangular is a fair-sized element which forms about half of the posterior third of the outer side of the jaw. It is very much larger than Watson believed. Posteriorly it rests on the articular, and articulates below with the angular and in front with the dentary and the coronoid. It forms much of the outer border of the upper opening of the jaw. There is a small foramen in the posterior part of the bone, but it is variable in position.

The articular is fairly large. It has on its upper side two hollows for the two convexities of the quadrate. There is a very short posterior process. In front is clasped by the surangular, the angular, and the prearticular.

In text-fig. 4 are given a number of sections across the jaw which show the relations of the bones.

*a.a.* is a section across the jaw at the 9th tooth. The two main bones are the dentary and the splenial. A small part of the anterior end of the angular is seen.

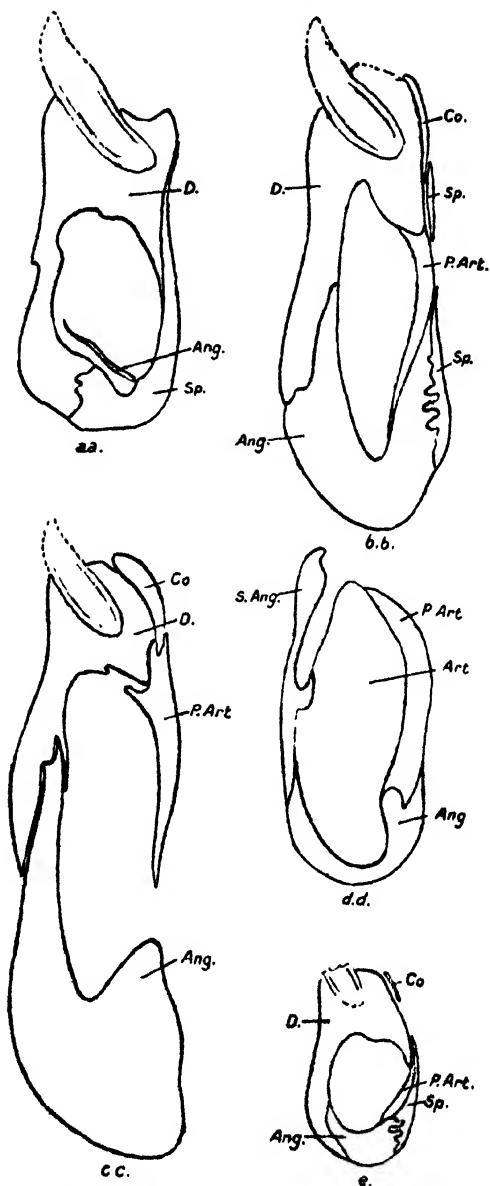
*b.b.* is a section across in region between the 15th and 16th teeth. The dentary is still seen to be large, but the lower part of the jaw is now seen to be formed by the angular. Two small parts of the splenial are seen: the lower firmly articulating with the angular; the upper lying on the dentary and the coronoid. The prearticular is a fairly large element, filling the gap between the dentary and the angular. The coronoid is seen as a small splint-like bone lying on the dentary.

*c.c.* is a section from the third last tooth downwards and backwards to behind the point of the horn. The largest element in this section is the angular. The dentary is still very large, and it articulates with the three other elements. The prearticular forms much of the inner side of the jaw. The foramen which opens into the jaw is seen cut across between the prearticular and the angular. The coronoid is seen resting on the dentary, and articulating also with the prearticular.

*d.d.* is a section through the posterior part of the jaw near the anterior end of the articular. The size of the articular varies greatly with the age of the jaw. In young jaws much of the



Text-fig. 4.

Sections of the jaws of *Pareiasaurus* sp. About  $\frac{1}{2}$ .

anterior part remains cartilaginous. In old jaws, as the one here sectioned, the anterior part is ossified. This large articular is seen clasped by the prearticular on the inside, the angular below, and the surangular on the outer side. Between the surangular and the articular is seen a deep cavity. This is the posterior part of the upper opening into the jaw.

c. This represents a section through the jaw of a young *Pareiasaur* intermediate between sections *a.a.* and *b.b.* The firm articulation of the splenial with the angular is seen. There are also seen the anterior ends of the coronoid and prearticular.

It is impossible at present to do much in tracing the affinities of *Pareiasaurus* from the jaw-structure, as we know so little of the jaw-structure in other Anapsidian reptiles. The jaws of *Pantylus* and *Procolophon* are adequately known, but in no other "Cotylosaurs." *Pantylus* is much more primitive in retaining the Amphibian preangular. The prearticular bone and the general arrangement of the bones of the posterior half of the jaw are fairly similar in *Pareiasaurus* and *Pantylus*. But this arrangement is the very primitive one found in the Labyrinthodonts, and also foreshadowed in the higher fishes. *Procolophon* has a jaw which, as shown by Watson, is essentially similar to that of *Pareiasaurus*, but the structure and relations of the bones are not yet fully enough known in detail to warrant any lengthy comparisons.

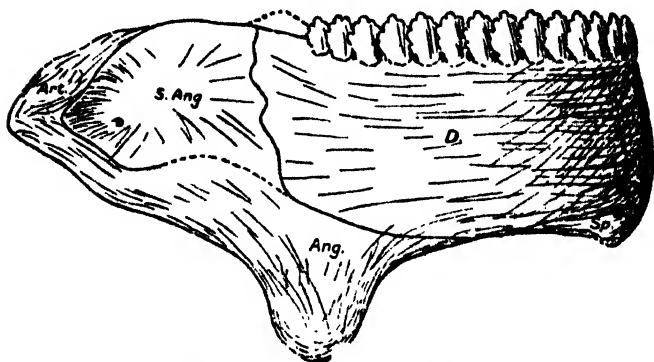
It is interesting to note that the jaw of *Pareiasaurus* differs very greatly from that of the jaws of the early Therapsidian reptiles. The structure of the shoulder-girdle and pelvis suggest affinity with the Therapsids. The jaw shows, as does also the skull, that the resemblances in the girdle are due to developments and not to affinity.

ADDENDUM, 30. 4. 24.—Since I sent off the above paper I have been able to examine another type of Pareiasaurian jaw. The jaw above described agrees with Owen's *Pareiasaurus bombidens* in having 20 teeth in each jaw; and comes from the same locality. We are thus probably justified in referring it to Owen's species. The jaw which I am now figuring comes from a somewhat lower locality, and differs in having 14 or possibly 15 teeth. The two jaws also differ so greatly in proportions that it seems likely we will ultimately have to place them in different genera or subgenera. But we will require to know much more than we at present know before we will be able satisfactorily to classify the Pareiasaurs.

The teeth in this new species are considerably larger than in *P. bombidens* and the broad crowns overlap. In *P. bombidens* the teeth ought to have been shown overlapping to a slight degree.

I give figures of two nearly perfect teeth showing the rounded cusps—one a tooth of *P. bombidens*; the other a tooth of *P. strubeni*.

Text-figure 5.



Mandible of *Pareiasaurus strubeni* Br. About  $\frac{1}{2}$  nat. size. The front half of the dentary is very much foreshortened. This mandible is that of a young specimen about  $\frac{2}{3}$  of adult size.

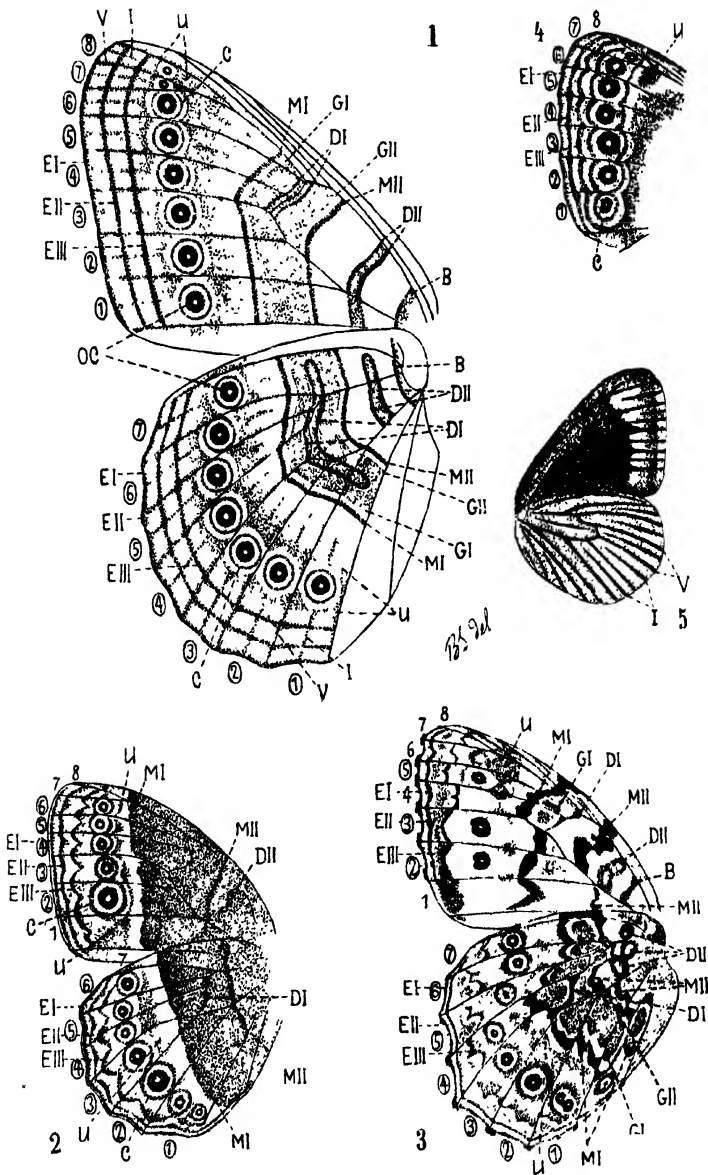
Text-figure 6.



- A. 5th tooth of right mandible of *Pareiasaurus strubeni* Br.  
Outer view. Nat. size.  
B. 9th tooth of left mandible of *Pareiasaurus bombidens* Ow.  
Inner view. Nat. size.

The new species I am naming in honour of Mr. F. P. T. Struben, the proprietor of Abraham's Kraal, and to whose interest in palaeontology we owe so much.

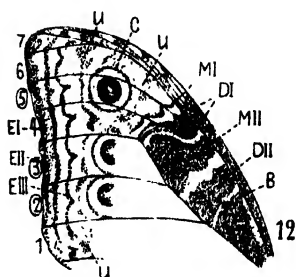
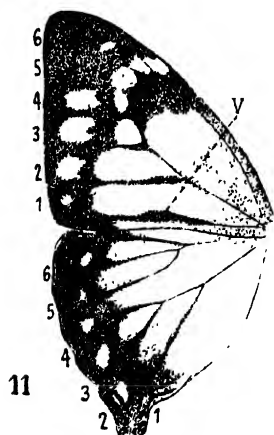
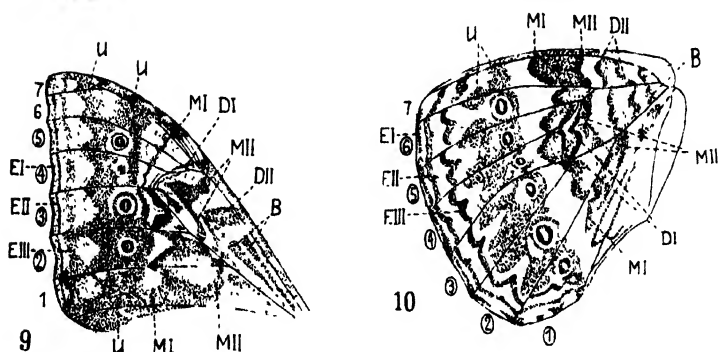
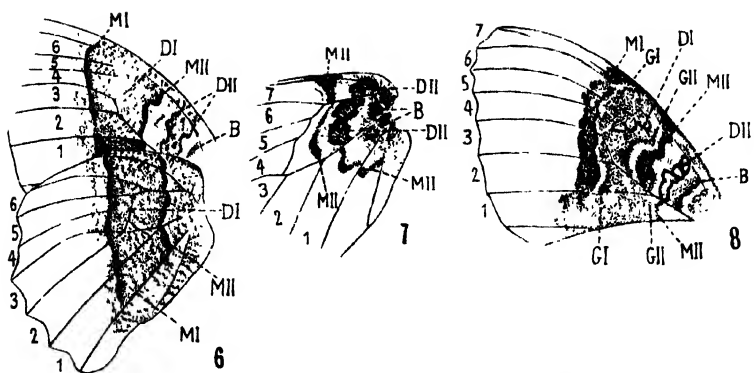




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GROUND-PLAN OF WING-PATTERN IN NYMPHALIDS AND OTHER RHOPALOCEROUS LEPIDOPTERA.

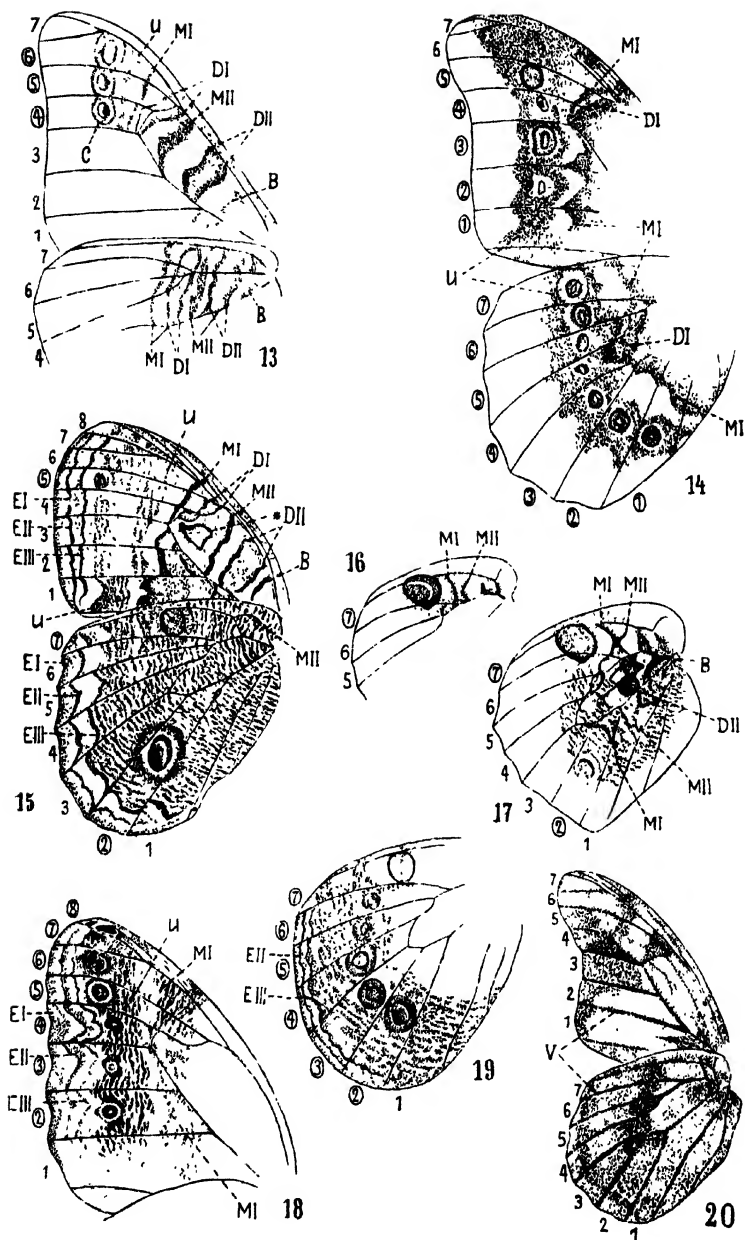




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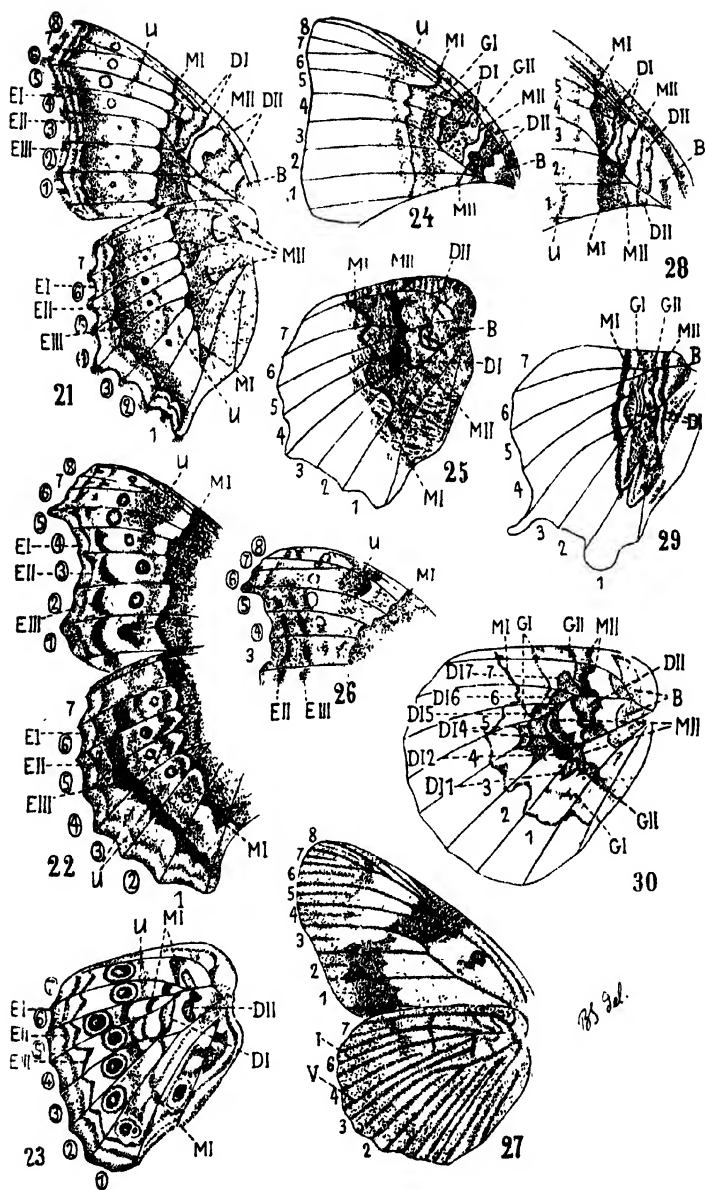




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GROUND-PLAN OF WING-PATTERN IN NYMPHALIDS AND OTHER RHOPALOCEROUS LEPIDOPTERA.





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GROUND-PLAN OF WING-PATTERN IN NYMPHALIDS AND OTHER RHOPALOCEROUS LEPIDOPTERA.

21. On the Ground-plan of Wing-pattern in Nymphalids and certain other Families of the Rhopalocerous Lepidoptera. By B. N. SCHWANWITSCH \*, Zoological Laboratory of the University of Petrograd, Russia.

[Received February 1, 1924: Read March 18, 1924.]

(Plates I.-IV.†)

I. INTRODUCTION.

The colour-pattern of the wings of the Lepidoptera has been treated in many experimental studies and an immense number of descriptive works, and yet we have but comparatively few studies considering the pattern as such. Its investigation has scarcely begun, although during these last years several authors, such as G. F. van Bemmelen‡, J. Botke§, A. Braun||, J. C. de Meijere¶, and N. J. Kusnezov\*\*, have published works on this subject. The wide extent of the subject sufficiently explains its present state.

This preliminary communication is not the place for giving a detailed survey of the relevant literature, and I think it sufficient to say that until now the well-known investigations of Th. Fierer†† continue to be the most important, and that the majority of authors consider the dark stripes crossing the wings as the basis of the pattern of the Lepidoptera. Fierer counts 11 such stripes, Kusnezov 22, van Bemmelen and Braun 7.

It must be remarked that not one of the authors who have studied the pattern of the Lepidoptera has figured any general schema of it, with the exception of the old and happy but little-elaborated schema of Herrich-Schaeffer for the Noctuiden‡‡, and the schema of W. Rothschild and K. Jordan§§ for two highly-specialized genera of Nymphalids (*Charaxes* and *Eulepis*). The rest of the authors either homologize the different patterns, as, for instance, F. Dixey||| in his standard memoirs, or, taking

\* Communicated by N. D. RILEY, F.Z.S.

† For explanation of the Plates, see p. 528.

‡ Proc. Acad. Wet. Amsterdam, xviii. 1916; xx. 1918; xxi. 1919; xxi. 1919 a; xxii. 1920; xxii. 1920 a; xxiii. 1921. Zool. Anz. 1916, 1921.

§ Tijdschr. Ned. Dierk. Ver. (2) xv. 1916-1917.

|| Jour. Acad. Nat. Sc. Philadelphia, (2) xvi. 1914.

¶ Tijdschr. Entomologie, liv. 1916.

\*\* "Faune de la Russie et des pays limitrophes fondée principalement sur les collections du Mus. Zool. de l'Acad. Sc. Petrograd." Insecta Lepidoptera, i. 1915.

†† Orthogenesis der Schmetterlinge (Leipzig, 1897). Die Artbildung u. Verwandtschaft bei d. Schmetterlingen (Jena, 1889, 1893).

‡‡ See Kusnezov, l. c.

§§ Novit. Zool. v. 1898.

||| Trans. Entom. Soc. London, 1890, 1894.

as a base any existing pattern which they consider as allied to their schemas, they have these latter in mind only. So, *e. g.*, does Eimer. V. Shelford \*, however, in his interesting investigation of the Tiger-Beetles, gives what I consider to be the convenient method of investigating a phenomenon of such manifoldness: to construct an abstract schema from which the actual phenomena may be derived.

I use the same method, though, owing to the war and revolution, I did not get acquainted with the memoir of Shelford until a long time after the beginning of my work.

This paper contains an attempt to construct a schema or prototype of the wing-pattern for several allied families of the Rhopalocerous Lepidoptera, chiefly the Nymphalids, Satyrids, Morphids, and Brassolids.

In my investigations I have availed myself of the collections of the Zoological Museum of the Academy of Sciences at Petrograd, as well as the small collection of the University of Petrograd, and sometimes also the atlas of A. Seitz †. I am indebted to the Administration of the Zoological Museum, and chiefly to Mr. N. Kusnezov, Custodian of the Lepidopterological Department, for permission to study its extensive collections.

## II. THE SCHEMA OR PROTOTYPE OF THE WING-PATTERN.

The present study is free from the tendency which may be traced throughout the whole morphology and comparative anatomy of the second half of the nineteenth and the beginning of the twentieth century—the tendency to construct the schemas of the organization of different groups of the animal world and call them the hypothetical ancestors of these groups. I think a morphological schema necessary only in order to show which of the features of the various organisms under investigation are common to them, and to make clear the general plan of their structure. In what relation our plan of structure of the now living organisms stands to that of their extinct ancestors is chiefly a palæontological question, not to be decided without palæontological methods if we want to avoid introducing into zoology too many hypotheses. This point of view, though not generally accepted, is supported by some of the most prominent contemporary biologists, such as O. Abel and others, and affords two advantages: firstly, we get rid of superfluous hypothetical ballast, and secondly, by eliminating the ancestral element, we acquire much more freedom in the actual construction of schemas.

The schema or, as I think more convenient to call it, the prototype of the wing-pattern, shown at Pl. I. fig. 1, is constructed in accordance with the foregoing considerations. This purely

\* Illinois Biol. Monogr. iii. No. 4, 1917.

† Die Grossschmetterlinge d. Erde.

abstract construction was altered repeatedly as my studies proceeded, and is liable to undergo many more alterations with their further progress. In its present form, somewhat differing from that formerly published\*, it is but an approximate, may be incorrect, reproduction of that ground-plan of the wing-pattern of the families mentioned, the finding of which is the purpose of my studies. I do not attribute to it any ancestral meaning.

In the same sense as N. Kusnezov†, I understand the wing-pattern of the butterfly to be formed by the ensemble of the dark, chiefly melanic, stripes and spots. The light, often vividly-coloured background on which they are situated I look upon as a substratum without morphological importance, and do not take it into consideration. The limits set to my investigation are exclusively and purely methodological, and I by no means prejudge any decision on the nature of the relation existing between the pattern and the background.

The stripes and spots forming the prototype of the wing-pattern—in other words, the components of the pattern—shown at Pl. I. fig. 1, according to their relation to the wing-nervures, are divided into longitudinal and transverse. The longitudinal ones are parallel to the nervures, the transverse ones are disposed transversely to the nervures. The longitudinal stripes are of two kinds: they may be called venous (V.) when they follow along the nervures, and intervenous (I.) when they run between the nervures along the middle line of the respective cells.

The transverse components represent much greater variety. Along the outer margin there are three parallel stripes, which, beginning with the outermost, we designate as Externa I. (EI.), Externa II. (EII.), and Externa III. (EIII.). After them comes a chain of eye-spots (Ocellate (OC.)), one in each cell. In view of the great independence of the separate eye-spots, each of them is marked with a number corresponding to the number of its cell. For my purpose the system of numeration used by English authors is very convenient, and applying it, we have on the fore-wings eight and on the hind-wings seven eye-spots, the nearest of them to the hind margin being counted as the first. The eye-spots represent a circle, with a light remnant of background (the pupilla of the systematists) in its centre. The eye-spots 7 and 8 of the fore-wing are considerably smaller than the rest of them, owing to their cells being narrow. Each spot is surrounded by a circle (C.) forming an independent component. The eye-spots 7 and 8 of the fore-wing have no circles. The next component is the shade or Umbra (U.), a broad ribbon-like band with diffused outline, accompanying the chain of eye-spots along the whole extent of it, and bordering it on both sides, so that one part of the Umbra is situated between

\* "Observations on the Wing-pattern in *Rhopalocera*." Proc. 1st Congr. Russ. Zool. Anat. & Histologists, Petrograd, 1923 (note the incorrect English transcription of my name).

† L. c.

Externa III. and the eye-spots, the other is proximal to the chain of the eye-spots. The Umbra fills, as it were, the intervals between the eye-spots, and therefore its edges on their side repeat the outlines of the eye-spots or their circles.

The rest of the wing is occupied by a medio-discal system of stripes which is rather complicated in the interrelations of its parts. Its morphological axis is a broad bar lying on the nervures enclosing the so-called median or central cell, situated in the central region of the wing. These nervures N. Kusnezov \* calls discal; this cell we will also call discal. The first discal stripe (DI.) on the fore-wing is confined to the limits of these nervures; on the hind-wing it extends forward into the 7th cell and backwards into the 2nd and 1st cells. As the first discal stripe is very often found double, it is represented in the prototype as composed of two parts, a discal and a proximal one, bordering the discal nervures. The second discal stripe (DII.), situated in the proximal half of discal cell, is of the same structure. On the fore-wing it extends backwards into the 1st cell, on the hind-wing (only) forward into the 7th cell. The last stripe is the Basalis (B.), and crosses both wings at their bases.

Near the morphological axis formed by the first two discal stripes (DI.) passes a broad ribbon-like band formed of two pairs of stripes. One pair of stripes, termed the first and second *Mediae* (MI. and MII.), form the margins of this ribbon. The other pair lie between the *Mediae* (MI., MII.) on either side of the discal stripe (DI.), and are designated as first and second *Granulatæ* (GI. and GII.). The *Mediae* differ little from the other above-described components in their structure—i. e., in the density and character of arrangement of their pigment. The first *Media* (MI.) passes distally from the first discal stripe (DI.) and crosses all the cells of the hind-wing from the 1st to 7th and six posterior cells of the fore-wing, for the 7th and 8th cells of the anterior wing do not reach as far as *Media* I. The second *Media* (MII.) passes proximally to DI., and in its greater part it extends over the discal cells, while only a small number of marginal cells are crossed by it. These are the 1st and 2nd cells of the fore-wing, and the 1st, 2nd, and 7th of the hind-wing. Both *Granulatæ* have a structure different from all the above described. They are not so much stripes as boundary lines of a broad, rather faintly-pigmented area enclosed by them. The grain-like arrangement of the pigment on this area in some actually existing patterns has led me to term them *Granulatæ*. The arrangement of both *Granulatæ* almost entirely corresponds to the arrangement of the *Mediae*; thus *Granulata* I. runs closely parallel to *Media* I., and *Granulata* II. to *Media* II.

Thus the components DI., MI., MII., GI., and GII. constitute

\* *L. c.*

a certain system, one half of which repeats, as it were, the other half. The morphological axis of the system is constituted not so much by the first discal stripe as by the discal nervures. We observe that, with regard to them, all the stripes of the system symmetrically arrange themselves in pairs. Nearest to the nervures are the two halves of the discal stripe itself (DI.); considerably receding from them and symmetrical to one another are situated Granulata I. (GI.) and Granulata II. (GII.); and, lastly, on the periphery the system is limited by two symmetrical Mediæ (MI. and MII.) I must insist that in this place I do not apply the word symmetry in its usual meaning, because from a glance at the figure it is clear that being laid one over the other the two halves of the system would not coincide, as the shape of MI. is not that of MII., as it would be if reflected by a mirror. If we could alter the shapes of all the cells in a way that they would become symmetrical with the axis of our system, as was done by A. Mayer\* with the pattern of the Heliconids, our system would be quite symmetrical also in the shape of its components. But being laid on the asymmetrical cells it becomes bent, and its halves do not coincide if laid one on the other. This phenomenon is but a particular instance of curvilinear symmetry, at the present time the subject of a special investigation by Professor D. V. Nalivkin in the Academy of Mining in Petrograd.

Such are the components constituting the prototype. In this preliminary communication I put them in the most simple form, without considering some complications which are sometimes observed, as, *e. g.*, the dividing of the stripes into two parts, etc. which as yet are not sufficiently studied, but when they are, may considerably alter the given construction.

During my work it has proved of great practical convenience to construct the formulæ of the patterns in analogy with the teeth formulæ of the Mammals. By connecting all the letters indicating the components used in Pl. I. fig. 1 we get the formula of the pattern. At the same time, each wing has its own separate formula, and these are written one above the other with the horizontal line between them; above the line are written the indices of the fore-wing, and beneath it those of the hind-wing. The eye-spots, in consideration of their great independence from one another, are designated in the formula, each by its own number. But I do not introduce the indices of the circles into the formula of the prototype under consideration. It is written as follows:—

El. EII. EIII. OC (1. 2. 3. 4. 5. 6. 7. 8.) U. | MI. MII. GI. GII. DI. DII. B. | V. I.  
 El. EII. EIII. OC (1. 2. 3. 4. 5. 6. 7.) U. | MI. MII. GI. GII. DI. DII. B. | V. I.

\* Bull. Mus. Comp. Zool. Harvard Coll. xxx. 1890-1897.



### III. THE REALIZATION OF THE PROTOTYPE OF THE WING-PATTERN IN SEPARATE FAMILIES OF RHOPALOCERA.

The described prototype of the pattern is a purely abstract schema, and the fundamental character of its realization consists in its not being entirely realized in any species or individual. I even suppose that some of the combinations introduced into it are not realizable at all. But as the prototype does not pretend to an actual existence, this is not to be considered as an impediment. Passing from individuals and species to genera and families, however, we shall find within their limits an almost complete realization of the prototype. Examples will show this best.

#### (1) *Satyridæ*.

Although the *Nymphalids* represent the most important group of butterflies treated in this paper, we shall begin with the family of *Satyridæ*, because we observe in them greater simplicity of the relations, and shall leave to the end the *Nymphalids* as the more complicated group.

On the underside of the wings of the Asiatic *Satyrid*, *Mycalesis* sp. (Pl. I. fig. 2)\*, we find a pattern repeating the prototype to a considerable degree. On the outer border there are three parallel stripes undoubtedly repeating the first, second, and third *Externæ* (EI., EII., EIII.). All these stripes, except EI. of the fore-wing and especially the third *Externa*, form a denticle in each cell. Proximally from them passes the chain of eye-spots. These are very well developed, with a light pupilla in the centre and a circle round each (C.). As the eye-spots themselves sharply differ from the other components and moreover are numerous, I have not designated them on the figures by their indices, but whenever an eye-spot occurs in a cell, the figure indicating its number is surrounded by a ring. In the first cell of the hind-wing there are even two eye spots. The doubling of the components of the pattern in this cell has found consideration in literature, and is explained by the presence of a rudimentary nervure which subdivides this cell in two. But in order to avoid unnecessary complication I do not introduce this additional spot into the prototype. Beyond the eye-spots there is the *Umbra* (U.), rather broad in the middle cells of the hind-wing. A blank interval separates it from *Media* I. (MI.). This latter has a more rectilinear course than in the prototype, owing to its anterior and posterior ends being displaced distad. The whole area between *Media* I. and the wing-base is rather intensely pigmented, but there are still discernible on it *Media* II. (MII.) on both wings, the first discal stripe (DI.) on the

\* I wish to state that the identifications of the specimens, from which the drawings for the present paper were made, were taken from the collection and materials of the Zoological Museum as well as from the University collection. Besides, this question is not of first-rate importance for our purpose.

hind-wing, and the outer half of the second discal stripe (DII.) on the fore-wing. Apparently its inner half also exists, but it remains invisible owing to the thick hair which covers the wing-base.

So we find in the *Mycalesis* sp. quite a number of the components of the prototype, but numbers of them are wanting: first, the eye-spots in the 1st, 7th, and 8th cells of the fore-wing and in the 7th cell of the hind-wing (that is why the members of these cells are not provided with rings); secondly, the first discal stripe (DI.) on the fore-wing; thirdly, the basal stripes (B.), which are entirely absent; fourthly, there is not a single stripe of the *Granulatæ* (GI. and GII.); fifthly, the longitudinal stripes are entirely wanting, the venous (V.) and the intervenous (I.). On the other hand some of the present components are expressed either not typically or weakly. The course of the first Media is not typical, as has been already mentioned, and all the medio-discal components present are weak.

If we write down the formula of the pattern of *Mycalesis* sp., putting dashes in the places of the absent components, its aspect will be the following:—

$$\begin{array}{l} \text{EI. EII. EIII. OC (2. 3. 4. 5. 6. - -) . U. | MI. MII. - - - DII. - | - -} \\ \text{EI. EII. EIII. OC (1. 2. 3. 4. 5. 6. - ) . U. | MI. MII. - - DI. - - | - -} \end{array}$$

In this formula, out of 41 members composing the prototypical formula, 25 of them are present, the other 16 are wanting.

However, turning our attention to some other Satyridæ, we shall find there the components in which the *Mycalesis* sp. is deficient. For example, we find in the *Anadebis himachala* Moore (Pl. I. fig. 4) on its fore-wing almost a complete chain of eye-spots OC (1. 2. 3. 4. 5. 6. 7. -). But the 8th eye-spot I did not find anywhere in the family of the Satyridæ, which probably is due to their 8th cell being very narrow. Almost all the circles (C.) surrounding the eye-spots coalesced in the *Anadebis* into two stripes on either side of the chain. The 7th spot of the hind-wing, wanting in the *Mycalesis* sp., is present in the *Neope goschenkitschii* Men. (Pl. I. fig. 3), which has on the hind-wing a complete chain OC (1. 2. 3. 4. 5. 6. 7.). The first Media (MI.) of the same *Neope* has a more prototypical course than that of the *Mycalesis* sp. Its anterior and posterior ends are bent towards the wing-base as in the prototype. The prototypical course of MI. is somewhat disturbed on the fore-wing, where MI.3, i.e. the piece of the first Media situated in the 3rd cell, is torn off from MI.4 and displaced proximally. But in another unidentified species of the same genus (Pl. II. fig. 8) the course of Media I. suffers no interruption. The best development of the course of both Mediæ we find in *Mycalesis visala* Moore (Pl. II. fig. 6), where moreover on the fore-wing the second discal (DII.) and basal (B.) stripes are distinctly developed. Both *Granulatæ* we find in some species of *Neope*. In *Neope* sp. (Pl. II. fig. 8)

they are visible (GI, and GII.) on the fore-wing, and in *Neope goschkevitchii* (Pl. I. fig. 3) on the hind-wing; they have the characteristic appearance of faintly pigmented lines bounding a not very dark area enclosed between them. On these same patterns appear the sufficiently developed first discal stripe (DI.) of both wings, and in *Neope* sp. (Pl. II. fig. 8) DI. of the fore-wing is even double, as required by the prototype. The second discal (DII.) of the hind-wing is found in *Neope goschkevitchii* (Pl. I. fig. 3), but here it is broken up into three parts, of which two are situated in the discal cell and the third in the 7th one. Besides that, the hindmost of these three parts touches the discal piece of the second Media (MII.), which also is not prototypical. But in *Neope simulans* Leech (Pl. II. fig. 7) this discontinuity is only indicated; the entire stripe (DII.) forms one whole and does not touch Media II. (MII.). Here we see also a rather perceptible Basalis (B.) on the hind-wing, wanting in all the above-named butterflies.

Until now we have not seen any longitudinal components. But the pattern of the American Satyrid, *Lymanopoda acraeida* Btlr. (Pl. I. fig. 5), represented by Seitz on table 52 g in vol. v. of his Atlas, consists on the hind-wing exclusively of venous stripes (V.) following along the course of the nervures and of intervenous stripes (I.) between them, and on the fore-wing chiefly of these stripes.

It is apparent from the above that the components of the prototype which are absent in the *Mycalesis* sp. with which we began may be found in other representatives of the family Satyridæ, and that even if each of them realizes the prototype incompletely, yet it is almost completely realized within the limits of the family. This is particularly obvious if we write out the formulæ of several of the butterflies examined in those parts that interest us, and then sum them up in order to obtain the total formula of the family. In putting above the line the indices of the components of the fore-wing and beneath it that of the hind-wing, we get:—

*Mycalesis* sp. (Pl. I. fig. 2).

El. EII. EIII. OC (- 2. 3. 4. 5. 6. --).	U.   MI. MII. - - - DII. -   - -
El. EII. EIII. OC (1. 2. 3. 4. 5. 6. -).	U.   MI. MII. - - DI. - -   - -

*Anadebis himachala* (Pl. I. fig. 4).

OC (1. 2. 3. 4. 5. 6. 7. -).		

*Neope* sp. (Pl. II. fig. 8).

	MI. MII. GI. GII. DI. DII. B.

*Neope goschkevitchii* (Pl. I. fig. 3).

El. EII. EIII. OC (1. 2. 3. 4. 5. 6. 7. ).	U.   MI. MII. GI. GII. DI. DII. -   - -

*Neope simulans* (Pl. II. fig. 7).

\_\_\_\_\_ DIL. B. :

*Lymanopoda acraeida* (Pl. I. fig. 5).

	V.I.
	V.I.

**SATYRIDÆ.**

EL. EII. EIII. OC (1.2.3.4.5.6.7.-). U. | MI. MII. GI. GII. DI. DII. B. | V. I.  
EL. EII. EIII. OC (1.2.3.4.5.6.7.). U. | MI. MII. GI. GII. DI. DII. B. | V. I.

This total formula of the family Satyridæ differs from the formula of the prototype in the absence of but one component—the eye-spot within the 8th cell of the fore-wing. But, as we have already said, the absence of this very spot is not essential, as the 8th cell is too narrow. There are, indeed, other disparities with the prototype which are not shown by the formulæ. For instance, I have not found on the hind-wing of Satyrids either those pieces of DI. which must lie outside the discal cell, or a case of the latter being divided up into two; neither have I found on the fore-wings the piece of DI. which ought to be within the 1st cell. But it seems to me, even taking into account their absence, we must admit that in the family of Satyridæ the prototype is realized with sufficient completeness.

(2) **Morphidæ.**

Applying the same method, we will now consider the Morphidæ, restricting ourselves to their American representatives.

The under side of the hind-wing of *Morpho epistrophis* Hb. (Pl. II. fig. 10) shows, but for the absence of the longitudinal stripes, almost an entire reproduction of the prototype. We see three finely-developed Externæ (EI., EII., EIII.), the third of which forms in each cell a large denticle. A broad Umbra (U.) borders an almost complete chain of eye-spots. (The presence of eye-spots is designated on the figure by rings surrounding the numbers of corresponding cells.) In the chain, only the 7th spot is wanting. Further on there is a broad dark ribbon formed by both Mediæ (MI. and MII.). In the discal cell, enclosed between the two Mediæ, there is the double first discal stripe (DI.). Still further we observe the second broad discal stripe (DII.) reaching into the 7th cell, and, lastly, at the base of the wing there is the typical Basalis (B.). The formula of this wing may be written as follows:—

EL. EII. EIII. OC (1. 2. 3. 4. 5. 6. -). U. | MI. MII. - - DI. DII. B. | - -

Besides the components absent in the formula, we must point to the absence of the first Discalis in the 6th and 7th cells and the absence of both Discalia behind the discal cell, to the rectilinear course of the eye-spot chain, and to the sinuous course of the first Media.

The absent 7th eye-spot is found in *Morpho anaxibia* Esp. (Pl. III. fig. 14). In the same butterfly we observe a more prototypical curved course of the whole chain of eye-spots. Here it apparently stands in connection with the outline of the outer edge of the wing, which in *Morpho epistrophis* is nearly rectilinear and bent in *Morpho anaxibia*. The piece of DI. wanting in the anterior cells of *Morpho epistrophis* is present in *Morpho sulkovskyi* Koll. (Pl. III. fig. 13), where this stripe reaches the extremity of the 7th cell. Here, too, the dividing of the two Discalia can be better traced than in *Morpho epistrophis*, and MI. is not sinuous. But I have not been able to find in the posterior cells of the Morphids the pieces of both Discalia, the presence of which is required by the prototype. Likewise I have not been able to find the Granulatæ.

Turning to the fore-wing, we see that *Morpho perseus* Cram. (Pl. II. fig. 9) reproduces the prototype rather completely. All three Externæ (EI., EII., EIII.) are sufficiently prominent, with the exception perhaps of the third (EIII.), which is less pigmented than the other two, and has coalesced with the Umbra (U.) along the three posterior nervures. The broad Umbra is subdivided at its anterior end and denticulated at its distal border. There are only four eye spots, in the 2nd, 3rd, 4th, and 5th cells. The course of the first Media (MI.) is prototypical in the anterior cells, while in the middle of the 1st, 2nd, and 3rd cells it is proximally displaced, with the result that it gives the first Media a denticulated outline. The second Media (MII.) on the whole repeats the course of Media I. Attention need only be called to its considerable dislocation at the base of the second cell and the resulting sharp bending of its outline in the discal cell. Notwithstanding these differences, the broad ribbon formed by the two Mediæ is sufficiently conspicuous. The first discal stripe (DI.), though faint, is still clearly visible; the second one (DII.) is well expressed, but repeats the sharp bending of the second Media. The basal stripe is present, but has divided into two longitudinal stripes. The formula of the fore-wing of *Morpho perseus* is the following:—

EI. EII. EIII. OC (- 2. 3. 4. 5. ---). U. | MI. MII. - - DI. DII. B. | - -

The absence of some components and the other indicated divergencies from the prototype may be partly corrected.

A sharply-expressed EIII. with denticles identical with those we observe on the hind-wing of *Morpho epistrophis* (Pl. II. fig. 10) is found in *Morpho narcissus* Stgr. (Pl. II. fig. 12), where the other Externæ are also more strongly expressed than in *Morpho perseus*,

and moreover the indicated coalescence of EIII. with the Umbra on the posterior nervures does not occur. Of the absent eye-spots, the 6th is observed in *Morpho sulkovskyi* (Pl. III. fig. 13) and the rudimentary 1st in *Morpho anaxibia* (Pl. III. fig. 14). Both discal stripes in their divided state are well developed in the fore-wing of *Morpho sulkovskyi* (Pl. III. fig. 13), where the sharp bend of MII. and DII alluded to above is not present. A pattern more resembling that from which we departed is found in *Morpho narcissus* Stgr. (Pl. II. fig. 12), where these bends likewise are not found and the Basalis (B.) is not divided longitudinally. As for the Granulate, they, too, were not to be found in the fore-wing. The longitudinal components are also very feebly developed in the Morphids. *Morpho æga* Hb. (Pl. II. fig. 11) has conspicuous venous stripes (V.) along the nervures, though they are rather short on the hind-wing. But I was not able to ascertain the presence of intervenous ones. The venous stripes of *Morpho æga* manifest themselves well on the upper side of the wing, whereas all the other patterns treated are those of the under side. As I am convinced that there exists a close connection between the upper and under side designs, I do not consider this circumstance an obstacle to the inclusion of the venous stripes in the pattern of Morphids in general; but as the nature of this connection is sometimes very complicated, I must make this remark.

By summing up the formulæ of some of the patterns of *Morpho*, considered as we have done in the preceding paragraph, we get the following table:—

*Morpho perseus* (Pl. II. fig. 9).

EL. EII. EIII. OC (- 2.3.4.5. ---).	U.	MI. MII. - -	DI. DII. B.	- -
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*Morpho epistrophis* (Pl. II. fig. 10).

EL. EII. EIII. OC (1.2.3.4.5.6. -).	U.	MI. MII. - -	DI. DII. B.	- -
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*Morpho anaxibia* (Pl. III. fig. 14).

OC (1.2.3.4.5. ---).				
OC (1.2.3.4.5.6.7.).				

*Morpho sulkovskyi* (Pl. III. fig. 13).

OC (4.5.6. - -)				
-----------------	--	--	--	--

*Morpho æga* (Pl. II. fig. 11).

				V. -
				V. -

#### MORPHIDÆ.

EL. EII. EIII. OC (1.2.3.4.5.6. - -).	U.	MI. MII. - -	DI. DII. B.	V. -
EI. EII. EIII. OC (1.2.3.4.5.6.7.).	U.	MI. MII. - -	DI. DII. B.	V. -

In the total formula of the family there are wanting eight members. I think that at least part of them are likely to be found in a more extensive material than happens to be at my disposal, because in the collection of the Zoological Museum of the Academy of Sciences, the exotic material is considerably inferior in quantity to the Palearctic. For example I have found in one specimen of *Morpho æga* indications of both *Granulatæ*, but not distinct enough to justify taking this species into account just now. However, accepting the formula of the *Morphids* such as it is, it must be acknowledged that, with the exception perhaps of longitudinal components, the prototype in its essential parts is realized in this family with sufficient completeness.

The Asiatic *Morphids* are now considered as a subfamily—*Amathusiinæ*. I have studied them separately. The prototype is realized in them almost to the same degree as in *Morphidæ*, s. str., but not wishing to enlarge this paper, I confine myself to these remarks concerning them.

### (3) *Brassolidæ*.

In the purely American family of the *Brassolids* there are observed the same relations.

In *Opoptera acadina* Latr. (Pl. III. fig. 15) we find on the under side the following pattern:—The second and third *Externæ* (EII., EIII.) are sufficiently apparent, whereas the first (EI.) is considerably fainter, especially in the fore-wing, and is represented not by a sharply-outlined stripe, but by a diffuse darkening of the outer wing-margin. The chain of eye-spots is very reduced; only the 5th is present on the fore-wing, and the 2nd and 7th on the hind-wing. The *Umbra* (U.) is discernible only on the fore-wing, where it presents a broad ribbon, filling out the interval between EIII. and MI. and narrowing in its hind part. In the first cell it is darker than in the rest. The medio-discal system is also developed only on the fore-wing. The first *Media* offers the usual aspect except for its posterior end, which is displaced distally. The second *Media* (MII.) is well developed in its distal part, and in the first cell displaced proximally. The first discal stripe (DI.) is not large, but well developed and double. Between MI. and MII. there is a loop marked by an asterisk\*. An investigation of the genus *Opsiphænes*, on which I cannot dwell in this place, shows that this loop probably represents a separated part of MII. Further on comes the excellently developed and characteristic second *Discalis* (DII.), and lastly the *Basalis* (B.). The formula of the design of *Opoptera acadina* is the following:—

EI.	EII.	EIII.	OC	( - - - - 5 . - - - )	. U.		MI.	MII.	- -	DI.	DII.	B.		- -
EI.	EII.	EIII.	OC	( - 2 . - - - - 7 . )	- -		- -	- -	- -	- -	- -	- -		- -

There are wanting in this formula 26 members out of 41. Essential features are the absence of almost all the eye-spots and

the whole medio-discal system on the hind-wing, for though at the supposed place of the latter there are light-coloured areas, it is not possible to say with certainty to what they correspond. Besides this, our attention is attracted by the fact that the 7th eye-spot of the hind-wing is displaced too much proximally. This may lead one to doubt its belonging to the prototypical chain. But an investigation of several more representatives of Brassolids completes to a considerable degree the poverty in members of the formula of the *Opoptera*.

Thus on the fore-wing of *Caligo prometheus* Koll. (Pl. III. fig. 18) we see, first, EI. much more sharply outlined than in *Opoptera*, and secondly, and this is of the greatest importance, the chain of eye-spots is here present in its entirety, with the exception only of the 1st spot. It must be pointed out that only the 2nd, 3rd, and 5th spots have the typical aspect, while the rest of them are degenerate, and of the 6th, for instance, there remains chiefly the large pupilla having the crescent-like shape characteristic of the Brassolids. Nevertheless it is quite clear that *Caligo* has a chain:—

OC (- 2 . 3 . 4 . 5 . 6 . 7 . 8 .).

*Catoblepia berocynthus* Cram. (Pl. III. fig. 19) has on the hind-wing an almost complete chain, represented by the formula:—

ÖC (- 2 . 3 . 4 . 5 . 6 . 7 .).

Here, too, several spots—chiefly the 6th—are degenerate, but their presence is still apparent. It is evident, too, that the above-indicated proximal position of the 7th spot in *Opoptera* is due to the considerably bent course of the whole chain on the hind-wing of Brassolids.

The medio-discal system of the hind-wing is present in *Opsiphanes inviræ* Hübn. (Pl. III. fig. 17). When tracing the course of the two Mediae (MI., MII.), beginning by the posterior end, we see that they cross the first cell, after which MI. passes through the second cell into the corner of the third one, and MII. enters through the corner of the second cell into the discal one, where it bends thrice at right angles and with its anterior end coalesces with the large dark DII. The first Media (MI.) having passed into the 3rd cell disappears in it, is absent in the 4th, appears again in the 5th, and through the 6th comes out into the 7th, reaching its limit. Its whole course leaves the impression (here I by no means intend to speak of the nature of the process) that Media I. is moving towards the wing-base, but is not able to cross the discal nervures lying on the way, and therefore begins to envelop the discal cell on either side, and at the place of the greatest "tension"—namely, the apex of the cell—disappears entirely, breaking up, as it were. In the 7th cell, besides MI. there is found also MII., the two having coalesced in the middle of the cell. This coalescence obscures the picture, but in another



specimen of the same species (Pl. III. fig. 16) it is absent, and both *Mediae* pass through the entire 7th cell independently of each other.

I cannot ascertain the presence of the first discal stripe in *Opsiphanes*, though there are indications of its existence, but the second one (DII.) is very strongly developed. It is divided into anterior and posterior halves dislocated from one another. This dislocation repeats the bend of the above-treated piece of *Media II.* and does not represent anything exceptional. A similar configuration of DII. exists for instance in *Neope goschkevitschii* (Pl. I. fig. 3). In *Opsiphanes inviræ* the second *Discalis* apparently has no extra-discal parts, but there is a sufficiently discernible *Basalis* (B.). The formula of the medio-discal system of the hind-wing of *Opsiphanes inviræ* is the following:—

MI. MII. — — DII. B.

The last of the *Brassolids* we have to consider is *Penetes pamphanis* Doubl. (Pl. III. fig. 20); it has a design in which the presence of venous stripes (V.) on both wings is quite obvious. There are no intervenous stripes, for I cannot consider the small stripe at the base of the fore-wing sufficient for introducing this component into the formula.

Summing up the formulæ of the *Brassolids* dealt with, we have:—

*Opoptera acadina* (Pl. III. fig. 15).

El. EII. EIII. OC (— — — — 5. — — — —).	U.   MI. MII. — — DI. DII. B.   — —
El. EII. EIII. OC (— 2. — — — — 7. ). — —	— — — — — — — —   — —

*Caligo prometheus* (Pl. III. fig. 18).

OC (— 2. 3. 4. 5. 6. 7. 8. ).	— — — — — — — —
	— — — — — — — —

*Catoblepia berecynthus* (Pl. III. fig. 19).

OC (— 2. 3. 4. 5. 6. 7. ).	— — — — — — — —
	— — — — — — — —

*Opsiphanes inviræ* (Pl. III. fig. 17).

| MI. MII. — — — — DII. B. |

*Penetes pamphanis* (Pl. III. fig. 20).

	— — — — — — — —   V. —
	— — — — — — — —   V. —

#### BRASSOLIDÆ.

El. EII. EIII. OC (— 2. 3. 4. 5. 6. 7. 8. ). U.   MI. MII. — — — — DI. DII. B.   V. —
El. EII. EIII. OC (— 2. 3. 4. 5. 6. 7. ). — —   MI. MII. — — — — DII. B.   V. —

In this formula there are wanting 10 members out of 41. Only the *Granulatæ* and *Intervenose* are entirely absent: as regards the *Umbra* and *Discalis I.*, their presence on the fore-

wing gives us a right to expect their presence on the hind-wing. With no less right there may be expected the presence of eye-spots in the first cells of both wings. The material of Brassolids in the Zoological Museum of the Academy of Sciences is very scanty. At my disposal there were no more than 173 specimens, but I suppose that with more material the formula of the family could be completed and the homologies of the components shown more easily. Nevertheless, even the analysis given justifies the assumption that our prototype is realized in the family of Brassolidæ in its main features.

#### (4) *Nymphalidæ*.

Let us now turn to the last and most extensive of all the families treated in this study—the Nymphalids.

The pattern of the under side of *Precis ceryne* B. (Pl. IV. fig. 21) to a considerable degree repeats the prototype. The three Externæ (EI., EII., EIII.), though not very prominent in the greater part of their extent, are yet sufficiently clearly expressed within the 1st cell of the hind-wing. The eye-spots are rather small, but their chain is very complete; only the 7th is missing on the fore-wing, and the 1st and 7th. on the hind-wing. On the proximal side they are bordered with an Umbra (U.), faint but clearly discernible. The first and second Mediæ (MI. and MII.) are very sharply delineated on the fore-wing, where between them is enclosed the first Discalis (DI.), which, however, is not prominent. On the hind-wing the first Media (MI.) is expressed with sufficient clearness, while the second one is discernible only in the discal and the 7th cells. The formula of *Precis ceryne* is composed as follows:

$$\begin{array}{l} \text{EI. EII. EIII. OC (1. 2. 3. 4. 5. 6. - 8.). U. | MI. MII. - - DI. DII. B. | - -} \\ \text{EI. EII. EIII. OC (- 2. 3. 4. 5. 6. - ). U. | MI. MII. - - - - - | - -} \end{array}$$

Out of 41 members there are wanting 13, and many of the components present are expressed faintly.

Other Nymphalids complete these gaps.

For instance, in *Precis amestris* Dru. (Pl. IV. fig. 22) all three Externæ are well pronounced in their whole extent; likewise the chain of eye-spots and the Umbra (U.) are expressed more clearly than in *Precis ceryne*, but the components of the chain are the same. They are completed by *Precis archesia* Cram. (Pl. IV. fig. 26), which has on its fore-wing a very small but nevertheless distinct 7th eye-spot (OC 7), and by *Apatura montis* Edw. (Pl. IV. fig. 23), which has on the hind-wing a complete chain of eye-spots, including the 1st and 7th ones we are in need of. Its formula is

$$\text{OC (1. 2. 3. 4. 5. 6. 7.).}$$

The medio-discal system is well developed in *Doleschallia pratipa* Feld. (Pl. IV. fig. 24), where, besides the full set of sharply-pronounced medial and discal stripes, there are present both

Granulatæ (GI. GII.) having a sufficiently discernible granulated structure. Thus *Doleschallia* possesses a complete medio-discal system of the fore-wing:

MI. MII. GI. GII. DI. DII. B.

But the parts of MII. in the first and second cells are displaced in *Doleschallia* towards the base of the wing so as to be situated in the geometrical prolongation of the outer half of Discalis II.; moreover, Discalis II. itself does not appear with sufficient clearness in the first cell. *Adelpha cytherea* L. (Pl. IV. fig. 28) offers in this respect a more prototypical picture, where MII. and DII. behind the discal cell obviously continue in the first one.

The medio-discal system of the hind-wing is visible in *Vanessa io* ab. *fischeri* (Pl. IV. fig. 25), where between both Mediæ (MI., MII.) there is enclosed the discal stripe (DI.), and further on there is observed the second Discalis (DII.) and the small basal stripe (B.). The formula is

MI. MII. -- DI. DII. B.

The Granulatæ absent in *Vanessa io* ab. *fischeri* are very well expressed on the upper side of *Cyrestis earli* Distant (Pl. IV. fig. 29), where the complex

MI. MII. GI. GII. DI.

has quite a prototypical aspect, except that all these components are less bent than in the prototype. Here, in addition to the two halves of DI. running along each side of the discal stripes, there is one more small stripe between them, lying on the nervures themselves. It is not introduced into the prototype, though it occurs also on the fore-wing. The formula of the part of *Cyrestis earli* considered is

MI. MII. GI. GII. DI. - B.

In order to convince oneself of the existence of extradiscal parts of the first discal stripe postulated in the prototype, it is necessary to dwell on the considerably modified pattern of *Phyciodes mylitta* Edw. (Pl. IV. fig. 30). When we designate each part of Discalis I. lying in the given cell, by an arabic numeral corresponding to the number of its cell, we shall see, beginning from in front, that DI.7 has the aspect of an irregular cone which does not reach the anterior limits of its cell, DI.6 and DI.5 fill the bases of their cells, DI.4 is double and bars the terminal part of the discal cell, DI.3 is absent, DI.2 lies at the base of the 2nd cell in the shape of an irregular roundish spot, and likewise DI.1 lies in the anterior part of the 1st cell. Here the last two parts (DI.2 and DI.1) are of essential importance, as they have not been observed in any of the preceding families. Here, too, the situation, hue, and character of the pigmentation of these two spots clearly show that they form the posterior prolongation of DI.4. This consideration justifies the introduction of the post-discal parts of the first discal stripe—i. e., of DI (1 . 2 . 3) into the hind-wing of the prototype.

On this same wing (Pl. IV. fig. 30) we see a very well-pronounced Basalis (B.). Furthermore it must be remarked that here Granulata I. has broken at the point where it passes from the 5th into the 6th cell, and the broken ends have moved far away from one another, one of them in a basal, the other in a terminal direction. In the 2nd cell, Granulata I. has almost vanished.

All the Nymphalids treated are without the longitudinal components of the wing-pattern. In *Phyciodes actinotina* (Pl. IV. fig. 27) the pattern of the under side of both wings, especially of the hind-wings, consists chiefly of venous stripes (V.) accompanying the wing-nervures and of intervenous stripes (I.) running between them. The last part of the formula of this species is

V. I.

V. I.

By summing up the formulæ of the species examined as before, we get:—

*Precis ceryne* (Pl. IV. fig. 21).

El. EII. EIII. OC (1. 2. 3. 4. 5. 6. - 8.). U.	MI. MII. - - DI. DII. B.   - -
El. EII. EIII. OC (- 2. 3. 4. 5. 6. - ). U.	MI. MII. - - - - -   - -

*Precis archesia* (Pl. IV. fig. 26).

OC ( - - - - - 7. ). U.	- - - - -
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*Apatura montis* (Pl. IV. fig. 23).

OC (1. 2. 3. 4. 5. 6. 7. ). U.	- - - - -
--------------------------------	-----------

*Doleschallia pratipa* (Pl. IV. fig. 24).

- - - - -	MI. MII. GI. GII. DI. DII. B.
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*Vanessa io* nb. *fischeri* (Pl. IV. fig. 25).

- - - - -	MI. MII. - - DI. DII. B.
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*Cyrestis earli* (Pl. IV. fig. 29).

- - - - -	MI. MII. GI. GII. DI. - B.
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*Phyciodes actinotina* (Pl. IV. fig. 27).

- - - - -	- - - - -   V. I.
- - - - -	- - - - -   V. I.

#### NYMPHALIDÆ.

El. EII. EIII. OC (1. 2. 3. 4. 5. 6. 7. 8.). U.	MI. MII. GI. GII. DI. DII. B.   V. I.
El. EII. EIII. OC (1. 2. 3. 4. 5. 6. 7. ). U.	MI. MII. GI. GII. DI. DII. B.   V. I.

The summed-up formula of the family of Nymphalids does not differ from the formula of the prototype—i. e., all the components of the latter are present in Nymphalids. So in them, for the first time, we meet with a complete realization of the prototype.

#### IV. CONCLUSIONS.

We have seen that in the four families examined the prototype is realized either for the greater part or completely. What is the significance of it? I feel bound to repeat in this place that I entirely abstain from attempting to draw any phylogenetic inferences. The prototype being an abstract schema represents a purely methodological contrivance. Its whole purport consists in enabling us by means of it to find out the common characters scattered among the immense variety of patterns belonging to the families referred to. If we have, indeed, succeeded in finding these common characters, and in this way come nearer to the knowledge of the ground-plan of the wing-pattern, the prototype has a sufficient right to existence. I am, however, convinced that, even if all or the greater part of the homologies demonstrated above be correct, the prototype is nevertheless no more than a first approach to the solution of the question in which we are interested, and after further investigation will indubitably undergo alterations.

To what extent is the plan of pattern here treated common to Rhopalocera? Excluding Hesperidæ, which stand apart, and counting up the number of genera in Staudinger's 'Exotische Schmetterlinge',\* we get for the whole of the Rhopalocera a total of 435. Out of this, 218 genera fall to the families Satyridæ, Morphidæ, Brassolidæ, and Nymphalidæ, and to the other nine families 215 genera. Accordingly our four families include nearly half of all the genera of Rhopalocera. In our case it is the genera and not the species that are more important, as the genera in their pattern are very often homomorphous. It is sufficient to point to the genus *Argynnis*, in which many dozens of species have essentially the same pattern. Therefore we have some right to declare that more than half the Rhopalocera, s. str., have a considerable number of features common to their designs. But Rhopalocera form one of the largest groups of the whole order of Lepidoptera.

As for the remaining families, some of them are indubitably connected with our prototype. Already Eimer† has shown that in the Nymphalid genus *Phyciodes* designs arise peculiar to the family of Heliconidæ. The material of the Zoological Museum has enabled me to confirm the correctness of this statement. In the same genus there are patterns very nearly approaching those of the American Acræid *Actinote*, which is indicated by the name of *Phyciodes actinotina*, represented by fig. 27 (Pl. IV.). Therefore it is admissible to suppose that in regard to the pattern

\* O. Staudinger & E. Schatz, 'Exotische Schmetterlinge,' 1885-1892.

† 'Orthogenesis,' p. 195.

the families of Heliconidæ and Acræidæ stand in an immediate relation to the prototype. This is quite natural, considering the systematic relation in which both of them stand to the Nymphalidæ. A partial realization of the prototype indubitably takes place also in the remaining families of Rhopalocera, which are mentioned by Staudinger and Schatz (Papilionidæ, Pieridæ, Danaidæ, Neotropidæ, Lycænidæ, Libytheidæ, and Erycinidæ). Without much difficulty among these families there can be found species with well-developed venous and intervenous stripes, or only venous stripes. This has been pointed out by Eimer\*, who considers such designs as a special "Faechertypus." Universally known, too, are the spots on the discal nervures of a great number of butterflies, apparently corresponding to *Discalis* I. of our prototype. These spots are found also in Heterocera. The transverse stripes of the Papilionidæ and other families have served as a starting-point to the work of Eimer. Dixey has treated them elaborately in the family of Pierids†; Kusnezov‡ gives his own schema of them, starting with 22 stripes, the maximum number observed by him. Only a special investigation can show whether these stripes correspond to our prototype, or that the plan of their disposition is a different one.

If we have come to the conclusion that the pattern of the families of Satyridæ, Morphidæ, Brassolidæ, Nymphalidæ, and also the Heliconidæ and probably Acræidæ are united by a certain plan they have in common, then there arises the question, whether the great variety of patterns we observe in these families is connected with this plan. This question I hope to consider in a subsequent paper.

#### SUMMARY.

(1) A prototype (schema) of the wing-pattern is constructed (Pl. I. fig. 1), which is intended as a ground-plan of the pattern in the families Satyridæ, Morphidæ, Brassolidæ, and Nymphalidæ.

(2) The prototype is composed of a number of dark stripes and spots, which are designated by corresponding terms. The formula of the pattern may be obtained by writing together the indices of these terms.

(3) The prototype is realized only partially in existing patterns; the formulæ of the latter are incomplete.

(4) In each of the families mentioned a series of patterns may be found which complement each other, and in this way it may be shown that a family realizes the prototype with sufficient completeness. In summing up the incomplete formulæ of existing patterns we obtain a more or less complete formula of the family.

(5) The general significance of the prototype is strengthened by the fact that about a half of the Rhopalocerous (s. str.) genera (excl. Hesperidæ) belong to the four families studied.

(6) A partial realization of the same prototype takes place in other families of Lepidoptera.

\* 'Orthogenesis,' p. 172.

† *L. c.* 1894.

‡ *L. c.*

## EXPLANATION OF THE PLATES.

## PLATE I.

Fig. 1. The schema or prototype of the wing-pattern of Nymphalids and certain other allied families of Rhopalocerous Lepidoptera.

Key to the Lettering:—

B.—Basalis.	I.—Intervenosa.
C.—Circulus.	MI.—Media I.
DI.—Discalis I.	MII.—Media II.
DII.—Discalis II.	OC.—Ocellata (eye-spot). For
EI.—Externa I.	another designation of
EII.—Externa II.	eye-spots, see below.
EIII.—Externa III.	U.—Umbra.
GI.—Granulata I.	V.—Venosa.
GII.—Granulata II.	*—See page 520.

The arabic ciphers designate numbers of border cells.

The ring encircling the arabic cipher designates the presence of an eye-spot in a given border cell.

The remaining figures except fig. 5 are made with a drawing camera from the specimens of the Zoological Museum of the Russian Academy of Sciences at Petrograd, and represent the under sides of wings or parts of them except figs. 11 and 29.

Figs. 2-5 represent a realization of the prototype of the wing-pattern in Satyrids. For lettering and general explanation, see fig. 1. 2, *Mycalopsis* sp.; 3, *Neope goschkevitchii* Men.; 4, *Anadebis himachala* Moore; 5, *Lymanopoda acraëda* Btlr. from Seitz's Grossschmett. d. Erde, Bd. v. pl. 52 b.

## PLATE II.

Figs. 6-8 represent a realization of the prototype of the wing-pattern in Satyrids (cont.). For lettering and general explanation, see fig. 1. 6, *Mycalopsis visala* Moore; 7, *Neope simulans* Leech; 8, *Neope* sp.

Figs. 9-12 represent a realization of the prototype of the wing-pattern in Morphids. For lettering and general explanation, see fig. 1. 9, *Morpho persens* Cram.; 10, *Morpho epistrophis* Hb.; 11, *Morpho æga* Hb. (upper side); 12, *Morpho narcissus* Stgr.

## PLATE III.

Figs. 13-14 represent a realization of the prototype of the wing-pattern in Morphids (cont.). For lettering and general explanation, see fig. 1. 13, *Morpho sulkowskyi* Koll.; 14, *Morpho anaxibia* Esp.

Figs. 15-20 represent a realization of the prototype of the wing-pattern in Brassolids. For lettering and general explanation, see fig. 1. 15, *Opoptera acadina* Latr.; 16 & 17, *Opsiphanes invira* Hübn.; 18, *Caligo prometheus* Koll.; 19, *Catoblepia bereocynthus* Cram.; 20, *Ponetes pamphanis* Doubl. Hew.

## PLATE IV.

Figs. 21-30 represent a realization of the prototype of the wing-pattern in Nymphalids. For lettering and general explanation, see fig. 1. 21, *Precis coryna* B.; 22, *Precis amestris* Dru.; 23, *Apatura montis* Edw.; 24, *Dolichallia pratypa* Feld.; 25, *Vanessa io ab. fischeri*; 26, *Precis arohaesia* Cram.; 27, *Phyciodes actinotina*; 28, *Adelpha cytherea* L.; 29, *Cyrestis earli* Distant (upper side); 30, *Phyciodes mylitta* Edw.

22. On a New Species of the Cestodarian Genus *Caryophyllæus* from an Egyptian Siluroid. By W. N. F. WOODLAND, D.Sc. (London), F.Z.S., Wellcome Bureau of Scientific Research.

[Received February 14, 1924: Read April 1, 1924.]

(Text-figures 1-4.)

Only one species of *Caryophyllæus* has been described hitherto from a Siluroid fish (*Auchenoglanis occidentalis* from the Anglo-Egyptian Sudan), and this was represented by a single immature specimen. Subsequent to the publication of my brief description of this form (Woodland, 1923) I discovered among the material collected by the late Dr. A. J. Chalmers, when Director of the Wellcome Tropical Research Laboratories at Khartoum, and kindly presented to the Wellcome Bureau by his successor, Major R. G. Archibald, several specimens of another new species of *Caryophyllæus* from another Siluroid, and the description of this form is the subject of the present communication. The new species is very similar in general organization to *Caryophyllæus filiformis* from *Mormyrus caschive* (Woodland, 1923), but it is worth describing, not only because it is a new species of an important genus, but because it illustrates the futility of regarding the character of the head as of generic value, and affords additional evidence for establishing the definitions of the genera *Wenyonia* and *Caryophyllæus* on a broad basis.

CARYOPHYLLÆUS CHALMERSIUS, sp. nov. Woodland, 1924.

Of this species I possess only two whole specimens, two anterior ends and one posterior end, and over a hundred transverse sections. This parasite was found in the Nile Siluroid *Oarias anguillaris* at Khartoum, and I propose to name it after Dr. Chalmers. The longer specimen (uncontracted) measured 19 mm. in length, with a maximum breadth (as mounted and possibly somewhat flattened on the slide) towards the hind end of the body of 1.6 mm.; the shorter specimen (extremely contracted) measured 8 mm. in length and 1.4 mm. in maximum breadth. I have already stated that *C. chalmersius* is very similar in general structure to *C. filiformis* (including the characteristic absence of post-ovarian vitellaria), and it only differs to a marked degree in the possession of a head which, curiously enough, very closely resembles that which I have previously described for *Wenyonia virilis*. Like the head of *W. virilis*, the head of *C. chalmersius* is relatively short (the head



## Text-figures 1-4.

## Reference Letters.

CO, cirrus aperture; EXCV, excretory vessel; ILMUS, internal layer of longitudinal muscles; IOV, isthmus of ovary; N, nerve; OV, ovary; SBCT, subcuticula; SCLMUS, outer layer of longitudinal muscle-fibres; SHGL, shell-gland; TES, testes; TEXTB, terminal excretory bladder; UT, uterus; VAG, vagina; VIT, vitellaria; VUO, vagino-uterine opening.

N.B.—The magnifications given are those at which the figures were drawn. The 5-cm. scale provided shows, when compared with an actual 5 cms., the amount of reduction which has occurred in reproducing the figures.

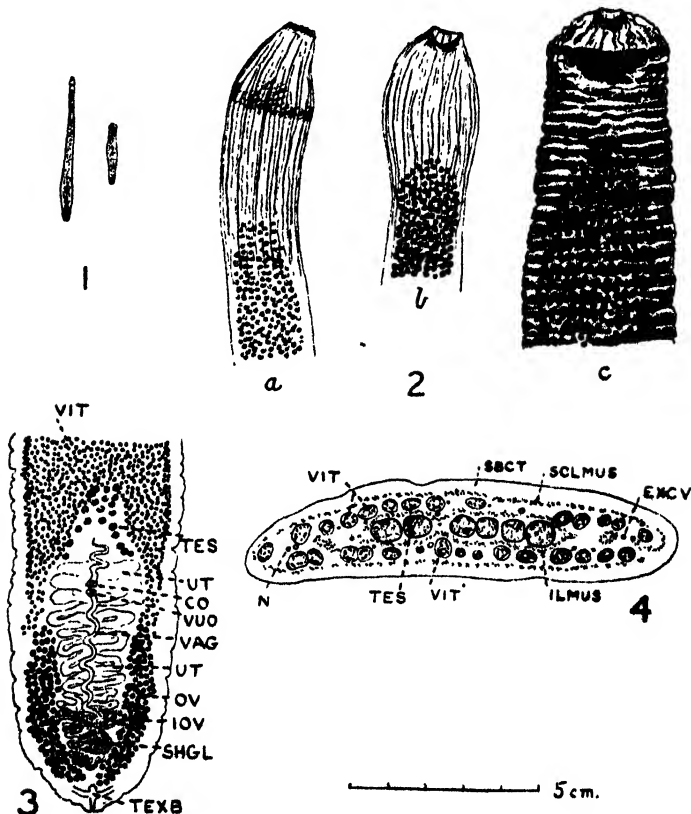
*Caryophyllaus chalmersius*.

Fig. 1 ( $\times 2$ ): the two entire specimens as mounted on slides.

Fig. 2, a, b, c ( $\times 24$ ): three heads, showing the longitudinal grooves and terminal depression. Fig. 2 c is much contracted. Figs. 2 a and 2 c represent the heads of my two entire specimens. The anterior vitellaria are shown.

Fig. 3 ( $\times 35$ ): the hind extremity of the contracted specimen, showing the chief organs. It is noticeable that the coils of the uterus extend both anteriorly to the genital openings and posteriorly to the shell-gland.

Fig. 4 ( $\times 78$ ): transverse section across the middle of the testicular region.

of my entire uncontracted 19 mm. specimen measured about 8 mm., and 1 mm. in the contracted 8 mm. specimen), is stout and muscular and very contractile, and its surface is marked by similar deep longitudinal permanent grooves lined by thick cuticle; it also often possesses a terminal cup-shaped depression (of varying size), and in some conditions a "base" is visible, as indicated by a dark circular band, the head then assuming to some extent the phalliform appearance which is so characteristic of *Wenyonia virilis*. I could detect no trace of "faserzellenstränge." The head of *C. chalmersius* thus differs greatly from that of *C. filiformis*, the head of this latter species being very long\*, thin, only slightly contractile, devoid of longitudinal grooves, and possessing "faserzellenstränge." In brief, *C. chalmersius* can succinctly be described as possessing the body of *C. filiformis* with a head resembling that of *W. virilis* attached.

My transverse sections across the testicular region† of *C. chalmersius* chiefly differ from those of *C. filiformis* in being much flatter (the breadth being at least 4 times the depth, whereas in *C. filiformis* the breadth is at most 2.5 times the depth); and this may not be due merely to difference of contraction, as is shown by the muscle-layers being in the same condition in many of the sections obtained from both species, and by the fact that in the hind testis region of *C. filiformis* the testes are usually arranged in two layers, upper and lower. These transverse sections also show, in one more instance, the distinctive features of the genus *Caryophyllæus*, viz. the annular arrangement of the vitellaria around the testes and the presence of an outer subcuticular and an inner epi-medullary layer of longitudinal muscles; and these two characters are probably *bona fide* ones in formally distinguishing *Caryophyllæus* from *Wenyonia*, the species of which latter genus only possess marginal strands of vitellaria and a single layer of longitudinal muscles.

Another feature which I have clearly observed in *C. chalmersius* is that for a considerable distance anterior to the genital apertures there are ten large longitudinal excretory channels, and this is doubtless also the case in *C. filiformis*.

The eggs of *C. chalmersius* measure (in balsam) 51.24–54.9 microns in length and 32.2–32.9 microns in breadth, and are

\* On re-examining my specimens of *C. filiformis* I find reason to believe that in all the cases in which I described (Woodland, 1923) the heads as being short the specimens are damaged. My previous figures (26 c and 26 d) are therefore misleading.

† I should here like to call attention to a mistake made in the drawing of *C. filiformis* in my previous paper. In fig. 25 the reference letters TES point to what are obviously vitellaria overlying the larger testes, which are not shown in the drawing (cf. fig. 28). The clear space separating the central from the marginal vitellaria (which actually does not exist) represents, of course, the space between the outer boundary of the underlying testis mass and the superimposed vitellaria at the edge of the body.

therefore slightly smaller than the eggs of most species of *Caryophyllæus*, though larger than those of *Wenyonia* species.

The species *Caryophyllæus chalmersius* may thus be defined as follows:—

The body measures about 8–19 mm. in length, with a maximum breadth of about 1·6 mm., and tapers slightly anteriorly when distended. The body is flatter than in *C. filiiformis* and is very contractile, but in the general organization closely resembles that of *C. filiiformis*. The head closely resembles that of *Wenyonia virilis*. The cirrus aperture is distinctly separated from the vagino-uterine aperture (*i. e.* not contiguous), and post-ovarian vitellaria are entirely absent. Eggs (in balsam) measure  $51\cdot2$ – $54\cdot9 \times 32\cdot2$ – $32\cdot9$  microns. Parasitic in the intestine of *Clarias anguillaris* (Siluridæ), Anglo-Egyptian Sudan.

Both *C. chalmersius* and the immature form previously described by me from *Auchenoglanis occidentalis* agree with *C. filiiformis* (from *Mormyrus caschive*) in the absence of post-ovarian vitellaria, and thus all three (all from the same locality) differ in this respect from all other previously-described species of *Caryophyllæus*.

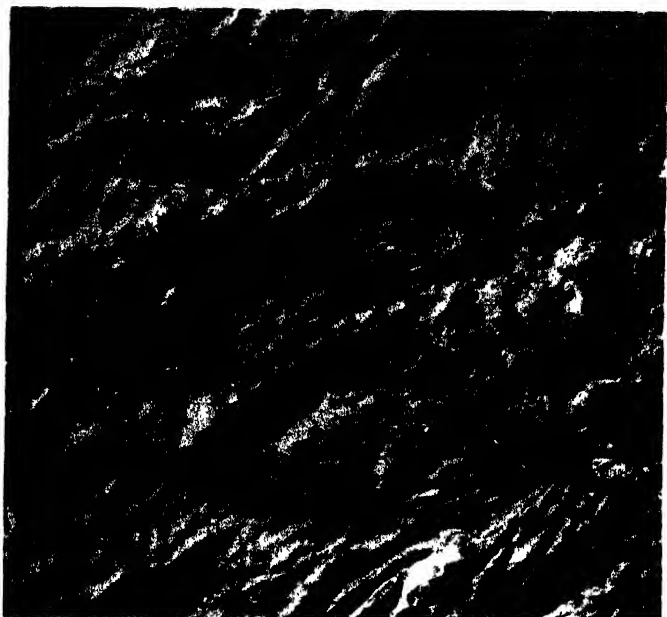
I would also add that in the formal definitions of *Caryophyllæus* and *Wenyonia* supplied in my previous paper I would include the further two distinctions above noted (annular arrangement of vitellaria and the two layers of longitudinal muscles).

In conclusion I should like to express my thanks to Dr. H. A. Baylis for his kindness in reading this paper before the Society and correcting the proofs during my absence from England.

#### *Literature Reference.*

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1.



2.

John Gale Sons & Danvers

ICHTHYOSAURIAN PADDLE.

23. Note on an Ichthyosaurian Paddle showing Traces of Soft Tissues. By C. W. ANDREWS, D.Sc., F.R.S., F.Z.S., British Museum (Natural History).

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[Received February 5, 1924: Read March 4, 1924.]

(Plate I.\*; text-figures 1, 2.)

The occasional preservation of portions of the integument of *Ichthyosaurus*, especially round the fins, has long been known. Buckland (1) so long ago as 1836 described and figured some portions of the skin from a specimen from Barrow-on-Soar, preserved in the Oxford Museum. In 1841 Owen (8) described and figured a hind paddle with well-preserved traces of the fringing fin, and this specimen was also referred to by Mantell (7). Another very well-preserved specimen of the front paddle was described and figured by Lydekker (6). These specimens will be further noticed below. E. Fraas (2-4) has given a very detailed account of the skin and fin border in a species of *Ichthyosaurus* from Holzmaden in Würtemberg, but his interpretation of the structures seen is not accepted by Reis (9), who considers that the cutis, epidermis, and scales of Fraas are actually portions of muscular tissues.

In the present paper I propose to give a short account of a specimen (B.M. R. 4550) from the Lower Lias of Barrow-on-Soar collected by Mr. S. L. Wood, and presented by him to the British Museum in 1917; together with some further account of the specimens described by Owen and Lydekker.

Mr. Wood's specimen consists of two slabs of rock, the larger of which bears some anterior ribs, the upper portion of the scapula together with the impression of the lower end, the humerus, split parallel to the surface of the slab, and a great part of the rest of the paddle in which most of the bones are represented only by the impressions of their surface. Judging from the scapula the limb is probably looked at from its inner aspect, so that the impressions of the paddle bones and the remains of the soft parts belong to the outer (upper) face of the paddle. Unfortunately the anterior border of the paddle is incomplete, but posteriorly traces of the fringing fin are preserved. The distal portion of the paddle is shown on the smaller slab, which forms the continuation of the counterpart of the larger one: on it ten or eleven of the distal paddle bones are preserved, becoming very small and widely spaced towards the lower angle which, unfortunately, is not completely preserved. On this fragment

\* For explanation of the Plate, see p. 537.

the structure of both the anterior and posterior fringing fin is shown, but neither is complete up to its margin.

On the larger slab traces of soft tissues are comparatively scanty. Behind the upper end of the humerus in the axillary region, there is an area of finely wrinkled skin traversed or underlain by bundles of whitish fibres which are presumably muscle-fibres: these run for the most part nearly parallel to the axis of the fin, but not in all cases. Opposite the posterior border of the carpal region there is also a patch of well-preserved skin, but the largest area is found fringing and overlapping the posterior border of the most distal part of the paddle preserved

Text-figure 1.

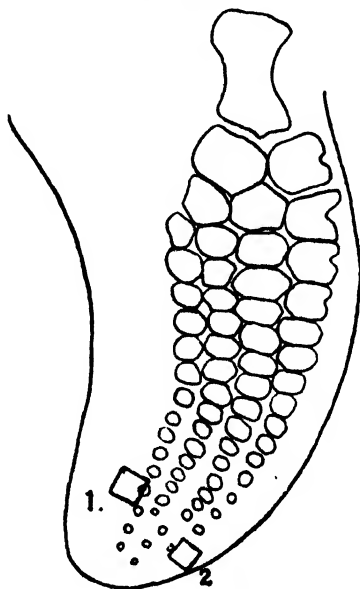


Diagram of an Ichthyosaur fin, showing the position of the areas figured in the Plate.

in this slab. The skin is here thrown into innumerable fine wrinkles and can be seen extending in between the postaxial rim of ossicles. The wrinkles run in a direction generally parallel to the long axis of the paddle, and unite frequently with one another. In places, especially towards the posterior border, bundles of muscle-fibres can be seen radiating in a general direction at right angles to the axis of the fin. The arrangement and structure of these muscle-bundles are much better shown in Lydekker's specimen, which will be referred to below.

It is on the smaller slab, bearing the distal portion of the

paddle, that the most interesting structures are seen (Pl. I. fig. 1). Here, as on the large slab, there is a broadly expanded posterior fin represented by a wide area of finely wrinkled skin which is marked by numerous patches of black pigment, many in the form of small rings about 5 or 6 mm. across: these may indicate that the integument was spotted in this region. In many places bands of muscle-fibres can be seen running in various directions.

The most remarkable structure is that seen on the front border of the fin (Pl. I. fig. 2). Here, running out about at right angles to the axis of the fin, there is a series of straight rod-like rays separated by intervals of 2 mm. These rods when not obscured by fragments of the wrinkled skin are quite

Text-figure 2.

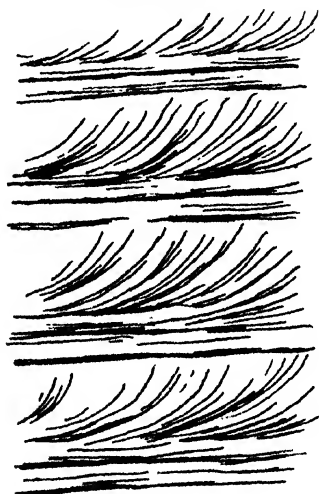


Diagram showing the arrangement of the rods and fibres figured in Fig. 2 of Plate.

definite structures: they sometimes seem to be formed by the fusion of several thinner rods, and although often broken up into short lengths, do not seem to have been definitely segmented. From the proximal border of each rod a series of fibres, presumably muscular, curve outward and upward to the distal border of the next rod higher up, so that the border of the fin appears to be divided into narrow areas, disposed at right angles to the axis of the fin and crossed by curved bundles of fibres, which sometimes appear to bifurcate. The rods themselves are continued on to the central portions of the paddle, and in a few cases they seem to have extended into the posterior fin.

Similar rod-like structures are described and figured by Owen,



who seems to have regarded them as marking the divisions between scales. Fraas also described similar structures which he likewise regarded as scales, an opinion from which Reis (9) dissents. The appearance of the specimen now figured seems to point to the presence of a series of muscular bundles separated by definite rods, which may be formed by the hardening of the connective tissue between the successive bundles into calcified or horn-like substance. The substance of which the rays are now formed seems to be probably some form of lime phosphate and appears similar to that replacing the muscle-fibres themselves. So far as I am aware, no instance of such rays has been recorded in other Reptilia, and I have not been able to find any comparable structure.

The specimen (R. 1664), also from Barrow-on-Soar, described by Lydekker, differs considerably from that now described. The parts preserved are a considerable portion of the thoracic and cervical regions, the left shoulder-girdle, and the proximal half of the fin split in the plane of the anterior and posterior fringing fin. This specimen is remarkable for the considerable extent to which the soft parts are preserved. Thus, between most of the ribs are masses of muscle-tissue, the fibres of which, for the most part, run obliquely down from the posterior border of one rib to the front of the next behind. In some places areas of wrinkled skin are preserved. The fringing fin of the paddle is very well preserved both in front and behind; the posterior lobe is about 2.5 cm. wide, the anterior about 1 cm. This anterior fin has a very sharply-defined anterior border, and its outline runs nearly parallel to the edge of the skeletal base: it is widest opposite the distal end of the humerus. In it considerable areas of muscle-fibres can be seen, for the most part running nearly directly outward to the anterior edge. In some regions the areas of soft tissue are divided up into small irregular partitions; these were regarded by Lydekker as indicating the presence of scales, but more probably they represented the broken ends of bundles of muscular fibres, there being no evidence of the existence of scales, and there is no trace of the division of the muscle into bands by parallel rods as described above, but this structure may have been confined to the distal end of the fin, here missing.

On the posterior side of the paddle, where the fin is much wider, it seems to have been supported by numerous bands of muscle-fibre running straight out from the skeletal base to the margin of the fin. The fibres of each bundle tend to converge towards the outer end, sloping outwards and towards the distal end of the fin. In the rod-bearing areas of the new fin described above the fibres slope outward and towards the proximal end of the fin. At their inner end the bundles are in contact, but as the fibres converge they become separated by a widening interval. Towards its outer end each bundle forms a narrow band, which at the actual margin seems to widen out and turn down along the

edge of the fin, forming with its fellows a more or less continuous border. There is no trace of the bifurcating rays of cartilaginous or albuminous horn-like substance described by Owen, although I have been unable to see them in his specimen, and his figure seems to be somewhat misleading.

*List of Papers referred to.*

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2. FRAAS, E.—Ueber die Finne von *Ichthyosaurus*. Bericht d. xxi. Versammlung des Oberrheinischen Geol. Vereins (1888) p. 31.
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7. MANTELL, G. A.—Petrifactions and their Teachings, 1851, p. 373, text-fig. 76.
8. OWEN, R.—A description of some of the Soft Parts with the Integument of the Hind Fin of the *Ichthyosaurus*, indicating the Shape of the Fin when recent. Trans. Geol. Soc. ser. 2, vol. vi. pt. 1 (1841), p. 199, pl. xx.
9. REIS, O. M.—Untersuchungen über die Petrificirung der Muskulatur. Archiv f. Mikros. Anatomie, Bd. 41 (1893), p. 492.

EXPLANATION OF THE PLATE.

Fringe of an Ichthyosaur Fin. Lower Lias, Barrow-on-Soar,  
Leicestershire.

Fig. 1. Posterior border of fin showing wrinkled skin and bands of muscle-fibres (see key plan, text-fig. 1).

Fig. 2. Anterior border of fringing fin showing the rays and connecting fibres (see key plan, text-fig. 2).

Both figures magnified about six times.



24. *Agrostichthys*, a new genus of Ribbon Fishes.

By W. J. PHILLIPPS, F.L.S., F.R.G.S.\*

[Received January 14, 1924 : Read March 18, 1924.]

(Text-figures 1 &amp; 2.)

A Ribbon Fish with the arrangement of the bones of the head showing considerable affinity to *Trachipterus*, and a body of the shape typified by *Regalecus*, but more elongate, was secured at Island Bay, Wellington, N.Z., in July 1921. It was later found to be identical with the fish described and figured by Benham (Trans. N.Z. Inst. xxxvi. p. 198, pl. ix., 1904) as *Regalecus parkeri*.

## AGROSTICHTHYS, gen. nov.

Body enormously elongated to  $22\frac{1}{2}$  times length of head; nearly 42 times greatest depth and 45 times depth at vent; 390 to 525 dorsal fin rays; teeth on head of vomer and on lower jaw; ventral reduced to single filament or marked by a minute depression if absent. Operculum extended downwards and

Text-figure 1.



Photo H. Hamilton.

*Agrostichthys parkeri* Benham. (Arrow marks position of anus.)

backwards with suboperculum below it; maxillary plate longer than deep; upper profile of head slightly convex; mouth protractile to  $\frac{1}{4}$  length of head.

The following key will serve to differentiate the three families of Allotriognathi represented in New Zealand seas:—

Length 6 to 12 times height; lateral line descending little below midway on side of body; ventrals present normally; eye large; teeth on vomer and both jaws; maxillary plate deeper than long

TRACHYPTERIDÆ.

Length 12 to 30 times height: lateral line descending to within  $\frac{1}{4}$  of height from ventral surface; ventrals represented by a single filament; eye small; teeth wanting; maxillary plate deeper than long

REGALECIDÆ.

Length over 30 times height; lateral line descending to within  $\frac{1}{4}$  of height of body from ventral surface; ventrals if present represented by a single filament; eye large; teeth on vomer and lower jaw; maxillary plate longer than deep

AGROSTICHTHYIDÆ.

\* Communicated by W. R. B. OLIVER, F.L.S., F.Z.S.

*Agrostichthys parkeri* is among the most strikingly attenuate fishes yet known from the ocean depths. The total length of the type was 45 in., while the greatest height was only 0.75 in. When fresh the Island Bay specimen was approximately 9 ft. in length, and  $2\frac{1}{2}$  in. high along the greater part of the anterior portion of the body. The lateral line is a raised tubular structure originating above the upper edge of the operculum at a

Text-figure 2.



Photo. H. Hamilton.

Head of *Agrostichthys parkeri* Benham.  $\frac{1}{2}$  nat. size.

point almost in line with the upper margin of the eye, and running downward towards the ventral surface and continuing along total length. The whole of the body is covered with a thick coating of minute silvery specks, each consisting of large numbers of minute crystalline prisms. Colour is slightly darker on the dorsal surface. Fins are bright scarlet.





John Bale Son & Danielsson L<sup>ds</sup>

MESOPLODON DENSIROSTRIS AND M. MIRUS.







MESOPLODON DENSIROSTRIS AND M. MIRUS.





John Bale Sons & Denisonson L

MESOPLODON DENSIROSTRIS AND M. MIRUS.





John Bale Sons & Danielsson L<sup>td</sup>

25. On *Mesoplodon* and other Beaked Whales. By Sir  
SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S.,  
F.Z.S.\*

[Received February 29, 1924: Read May 20, 1924.]

(Plates I-IV.†; text-figures 1-3.)

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The Whales belonging to the genus *Mesoplodon* are in certain respects among the least known of the Cetacea. They are presumably Oceanic forms, which from time to time become stranded on various coasts, but little has been ascertained of their mode of life or of their centres of distribution. Most of the species are represented by individuals which have been found singly, but there is evidence that they may occur in schools, as shown by the stranding of about 25 specimens of *M. grayi* on the Chatham Islands in 1875 (Oliver, 1922, p. 572). While certain species, such as *M. densirostris*, have a distribution extending beyond the limits of a single Ocean, others, such as *M. bidens* in the Atlantic and *M. grayi* in the Southern seas, seem to be more limited in their range, and so far as is known do not cross the Equator.

*M. bidens* and *M. grayi* have been recorded on a considerable number of occasions, but the remainder of the species are rarer in collections. The British Museum has recently had the good fortune to acquire examples of two of the rarest, *M. mirus* and *M. densirostris*, which form the special subject of the present paper.

\* Published by permission of the Trustees of the British Museum.

† For explanation of the Plates, see p. 587.

The known recent species of *Mesoplodon* appear to be nine in number.

1. *M. bidens* (Sowerby), 1804.
2. *M. densirostris* (de Blainville), 1817.
3. *M. europæus* (Gervais), 1848-1852.
4. *M. layardi* (Gray), 1865.
5. *M. hectori* (Gray), 1871.
6. *M. grayi* (von Haast), 1876 (Syn. *M. australis* and *M. haasti* Flower, 1878).
7. *M. stejnegeri* True, 1885.
8. *M. bowdoini* R. C. Andrews, 1908.
9. *M. mirus* True, 1913.

For 1, 3, and 7 in the above list, reference should be made specially to the important Memoir by True (1910); for 5 and 6 to Flower (1878); for 4 to Owen (1870-1889), Van Beneden and Gervais (1868-1879), and Turner (1880); and for 8 to Andrews (1908) and Oliver (1922). The synonymy of the other two species is given below. Kükenenthal (1914, pp. 119-122) has given a useful bibliography of *Mesoplodon*, and Forbes (1893) has described the remarkable alterations which take place in the ossification of the rostrum during growth. It seems unnecessary to discuss the numerous generic names which have been proposed for species of this genus. The subject has been summarized by Flower (1872, pp. 208, 209, Note 3), and I follow him in accepting *Mesoplodon* Gervais, 1850, with *M. sowerbiensis* de Blainville (= *Physeter bidens* Sowerby, 1804) as the type-species.

The principal cranial characters which were relied on by Flower (1878, pp. 417, 418) in distinguishing the species of *Mesoplodon* were:—

- (a) The presence, in certain species, of a deep longitudinal groove running along each side of the rostrum, commencing in a blind pit below the maxillary tubercle, and bounded above and below by prominent ridges.
- (b) The relative positions of the foramina for the exit of the facial branches of the second division of the fifth nerve, visible on the dorsal side of the skull.
- (c) The occasional occurrence of a row of small teeth in the upper jaw.
- (d) The position of the large mandibular teeth.
- (e) The form of the same teeth.

The structure described by Flower under (a) was termed by him the "basistrostral groove," and although he was not explicit on the subject it clearly represents the dentary groove of the upper jaw. From the researches of Abel (1905<sup>1</sup>, 1905<sup>2</sup>) and others it seems probable that the earlier representatives of the Ziphiidæ were provided with a long series of teeth in both the upper and lower jaws. In existing members of the family the upper teeth have disappeared, except for the occasional presence

of vestigial teeth. It is noteworthy that in *M. grayi*, in which the basirostral or dentary groove is better developed than in any other species, the upper jaw may be provided with a series of small teeth, situated near the middle of the rostrum (cf. Flower, 1878, pl. lxxii, fig. 2). It is not certain that these are always present, but Oliver (1922, pp. 572, 573) has described 17-19 teeth on each side in three specimens from the Chatham Islands and in one from New Zealand. Similar vestigial teeth have often been found in *M. bidens* and in other Ziphioids.

The only other species in which the dentary groove of the upper jaw remains distinct is *M. layardi*. Flower and others have stated that it is well developed in *M. densirostris*; but, although represented in this species, it can hardly be regarded as more than a vestigial structure.

It appears to me that sufficient attention has not been paid to the form of the base of the rostrum in distinguishing the species of *Mesoplodon*, although the proportions of the parts in question are variable and probably alter with age. At the antorbital notches, situated immediately in front of the orbits, the maxillæ are of considerable breadth; and, in accordance with the usual custom, the rostrum must be considered to commence at the notches, which are bounded on their median sides by the maxillary tubercles. Here the rostrum commonly contracts suddenly in width, and is often separated from the tubercles by a second sinus, which may be described as the inner notch. This does not occur in the genera *Berardius*, *Ziphius*, and *Hyperoodon*. The rostrum consists, in *Mesoplodon*, of the principal narrower portion, commencing at the inner notches, and of a broader basal portion, of relatively small extent. The dorsal maxillary tuberosities, which in the other genera represent the posterior ends of the great maxillary crests of *Hyperoodon*, extend in *Mesoplodon* into the maxillary tubercles.

In *M. layardi* the basal section of the rostrum is hardly represented. As seen in dorsal view (Brit. Mus. 69.4.5.2, skull-length 1090 mm., but the tip of the rostrum not quite complete\*), the anterior edge of the cranial part of the skull is almost transverse, but shows two sinuses or bays on each side of the middle line. The antorbital notch, the outer of these two, is the longer in a transverse direction, and is bounded externally by the antorbital tubercle. In the skull under consideration, a line joining the tips of the two antorbital tubercles of opposite sides passes completely in front of the whole of the region which represents the basal portion of the rostrum; and the slight maxillary tubercles, which limit the antorbital notch on the inner side, do not reach this line (Owen, 1870-1889, pl. i. fig. 2). It should be noted that this predominance of the antorbital tubercles occurs

\* This is the specimen described by Owen (1870-1889, pp. 12, 26, with figures of the skull, pl. i. figs. 1-6).



on the right side only in the young skull (length 25 in. = 635 mm.) figured by Turner (1880, pl. i. fig. 2). The well-developed basi-rostral groove commences in the maxillary tubercle and inner notch. Maxillary tuberosities are wanting, and there are no lateral maxillary flanges of the kind so obvious in *M. bidens* and certain other species.

In *M. bowdoini* also, as shown by the figures of Andrews (1908, pl. xiii.) and Oliver (1922, pl. iii.), the anterior edge of the cranial portion of the skull is nearly transverse, and as the two notches of each side are nearly at the same level the basal portion of the rostrum has hardly any length. The maxillary tuberosities are large, and the maxillary tubercle is strong, passing in front of the line joining the antorbital tubercles.

*M. densirostris* (Pl. I. fig. 1) is in marked contrast with both these two species. The shallow antorbital notches are followed by a long basal portion of the rostrum\*, ending rather suddenly without forming strong maxillary tuberosities, and separated from the narrow part of the beak by shallow inner notches.

The other species are for the most part intermediate between these two extremes. In *M. grayi* (Flower, 1878, pl. lxxi. figs. 1-3) and *M. stejnegeri* (True, 1910, pl. vi.) the basal portion of the rostrum is long, the inner notches are shallow, and owing to the small development of the antorbital tubercles the antorbital notches are not of the typical form. In *M. hectori* the broadened base is distinct†, the inner notches are barely represented, and the antorbital notches are definite bays. In *M. europæus* (True, 1910, pl. ii. fig. 1) the basal region of the rostrum is shorter, with strong maxillary tuberosities, shallow inner notches, and deep antorbital notches. In *M. mirus* (Pl. I. fig. 2) the characters are much the same, but the basal portion of the rostrum is still shorter, and the maxillary tubercles hardly extend in advance of the antorbital tubercles, which are larger than in *M. europæus*. In *M. bidens* (True, 1910, pl. i. fig. 1) the basal portion of the rostrum is short, the inner notches slight, the maxillary tubercles inconspicuous, the antorbital notches moderate, limited externally by small antorbital tubercles. Maxillary tuberosities are hardly indicated.

The form of the narrow part of the rostrum also differs according to the species. In *M. grayi* and *M. densirostris* (Pl. I. fig. 1), for instance, it is narrow, even proximally. In *M. bidens* and other species (Pl. I. fig. 2) with well-developed maxillary flanges it is considerably wider here than the distal part, into which it passes more or less regularly, the rostrum being thus an elongated, acute-angled triangle.

#### The relations of the bones in the region of the antorbital notch

\* Andrews's figures (1914, pl. xvii. figs. 1, 2) show a shorter basal region, and it is possible that the extent of its development is dependent on age.

† Flower's figure (1878, pl. lxxi. fig. 4) represents the part between the antorbital and inner notches as longer than is really the case.

seem to afford characters of systematic importance. Although there are numerous references in literature to the details observed in various species, I am not acquainted with any comparative treatment of the subject, and I describe accordingly the differences which appear to be significant. My study is based on the limited amount of material in the British Museum collection; and allowance must be made for the almost certain existence of individual variation. In each of the species represented by several specimens, particularly in *Hyperoodon*, *Ziphius*, *Mesoplodon grayi*, and *M. bidens*, I have found so close a general agreement that I am encouraged to believe that the points to which I call attention are of some importance.

The bones in question are the malar, lachrymal, frontal, and maxilla, in the antorbital region, where they have various relations to one another. A few remarks on the genera may be prefaced to the detailed accounts.

*Berardius* (True, 1910, pl. xxvi.) differs from the remaining Ziphioid genera in wanting the marked asymmetry, in certain bones, which is so characteristic of them. In this feature, as well as in retaining two pairs of large mandibular teeth, it may be regarded as the most primitive of the Ziphioids. The right premaxilla is hardly larger than the left, and the proximal end of neither is expanded. The maxillary crests or tuberosities are well developed, and resemble those of *Hyperoodon* except in being much smaller and in being directed obliquely outwards, instead of being vertical as in that genus. In a skull of *B. arnuxii*, 1113 mm. long, but with the tip of the rostrum not quite complete, in the British Museum (96.11.20.1) they reach a length of about 165 mm. The dorsal maxillary foramen is very large (40 mm. in length), the premaxillary foramen much smaller; and the two are nearly at the same transverse level. The nasals, which have a large horizontal component, are large and symmetrical, their median region not depressed, and they project dorsally beyond any of the other bones of the vertex (True, pl. xxviii.).

*Ziphius* (True, 1910, pl. xvi.) resembles *Berardius* in the possession of large nasals, not depressed in the middle, and with a long horizontal component. They are no longer symmetrical, as is shown by the obliquity of the suture which separates them. This is situated at the level of the vertex, and the front parts of the nasals project forwards above the nasal cavities. The right premaxilla is larger than the left, and the posterior ends are slightly expanded. The maxillary tuberosities (True, pl. xx.) are not unlike those of *Berardius*, but are less developed, and the very large maxillary foramen and the small premaxillary foramen agree with the corresponding apertures of that genus except in the fact that the premaxillary pair are in advance of the others.

*Hyperoodon* also shows a marked asymmetry in certain bones, for instance the premaxillæ and nasals, in both of which the right member is considerably larger than the left, as well as by

the oblique position of the nasal septum. The maxillary tuberosities take the form of enormous longitudinal and vertical crests, which increase in size with age, particularly in the males. The large maxillary foramen lies on the median side of the crest, and in a young skull from Weymouth (British Stranded Whales, 1917, No. 29), incomplete at the tip but with an estimated length of at least 790 mm., it measures 75 by 13 mm., the greater diameter being longitudinal. The premaxillary foramen is very small, and is situated opposite part of the larger foramen. The horizontal component of the nasals is much less developed than in the two preceding genera, and its sutural region, no longer on the level of the dorsal part of the skull, is considerably depressed. The lateral parts of the nasals are more elevated, and take part in the formation of the crests which are otherwise constituted by the expanded proximal ends of the premaxillæ, as in certain species of *Mesoplodon*. Their vertical component is large, and bounds the nasal cavities behind, their relations being best seen in young skulls. The right nasal of the Weymouth skull measures 75 mm. transversely and 92 mm. vertically, the corresponding measurements of the left nasal being 44 and 79 mm.

*Mesoplodon* resembles the last two genera in the asymmetrical development of its premaxillæ, nasals, and other parts. The nasals are most like those of *Hyperoodon*. The maxillary tuberosities are less developed than in any of the other genera, and may be vestigial or even wanting. The maxillary and premaxillary foramina are usually subequal in size, and are variable in their relative position. They are in most cases at about the same transverse level, but in *M. grayi* the premaxillary pair are considerably behind the others.

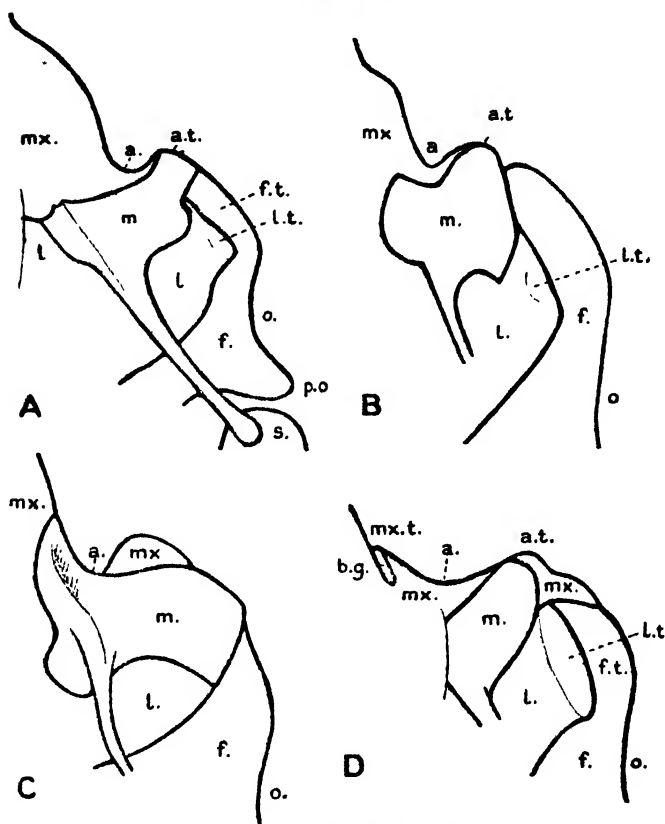
It appears probable from this survey that the Ziphioid Whales were originally provided with maxillary tuberosities of appreciable size; that the maxillary foramen was at first much larger than the premaxillary foramen; and that the two were situated at about the same transverse level; and, from what follows, that the malar originally reached the outer border of the antorbital region, while the outer border of the lachrymal was thickened.

It has been pointed out by Flower (1872, p. 204) that one of the distinctive features of the Ziphiidæ is the presence of "a distinct bone in the orbit, segmented from the posterior part of the malar, and probably the homologue of the lachrymal." The outer, thickened edge of this bone is well shown in figs. 1, 2, and 4 of pl. lxxii. of Flower's later Memoir (1878), lying immediately in front of the orbit, covered dorsally by the antorbital part of the frontal, and descending obliquely from in front backwards, where it helps to form the anterior margin of the orbit. Part of the malar is clearly shown in fig. 2 of the same plate as a small triangular bone, covered dorsally by the maxilla, at the antero-dorsal side of the lachrymal.

*Berardius* (text-fig. 1, A) is characterized by its large and heavy antorbital region, not much shorter than the orbit, which has its

dorsal border, as seen in dorsal or ventral view, strongly concave (True, 1910, pl. xxvii. figs. 2, 3). On the dorsal side (*B. arnuxii*) the maxilla is separated by an interval of 33 mm.\* from the edge of the orbit. In respect of its relatively strong zygomatic

Text-figure 1.



Antorbital region of skulls of Ziphioids (ventral view) in the British Museum.

A, *Berardius arnuxii*; B, *Ziphius cavirostris*; C, *Hyperoodon rostratus*; D, *Mesoplodon layardi*. a, antorbital notch; a.t, antorbital tubercle; b.g (in D), basistrostral groove; f, frontal; f.t, its thickened outer border; l, lachrymal; l.t, its thickened outer border; m, malar; mx, maxilla; mx.t, maxillary tubercle; o, orbit; p.o (in A), postorbital process; s (in A), squamosal.

portion, nowhere less than 9 mm. in width, the malar (m) of this genus may be considered more primitive than that of any other Ziphioid.

\* The measurements, as elsewhere, refer to skulls in the British Museum.

As seen in side view (True, 1910, pl. xxviii. figs. 1, 2), the outer edge of the frontal is specially thick (30 mm.), and it constitutes most of the antorbital region, overlapping\* the lachrymal (text-fig. 1, A, *l*). In the region of the antorbital tubercle (*a.t*) the large, transversely expanded anterior lobe of the malar (*m*) reaches the outer surface of the tubercle, along a length of 25 mm., the anterior lobe being about 105 mm. broad and 55 mm. long. The lachrymal (*l*) is unusual in extending round the median side of the anterior lobe of the malar. Its outer border is 55 mm. long, thick behind and fading away in front, its depth not nearly so great as that of the frontal edge overlapping it. As in most other Ziphioids, this characteristic thickened edge faces partly ventrally as well as outwards, and is thus visible in a ventral view. It should be noted that the malar does not bound the antorbital notch. The relations in *B. bairdii*, as shown by True (1910, pls. xxvii., xxviii.), seem to agree with those of *B. arnuxii* except that the thickened border of the lachrymal appears to reach the outer edge of the antorbital region.

*Ziphius cavirostris* (text-fig. 1, B), of which there are several British skulls† in the British Museum, agrees with *Berardius* in the fact that the frontal makes a specially large contribution to the antorbital region, the other bones of which show a considerable amount of incompleteness. The orbit is distinctly longer than the antorbital region. These features are well shown in the figures given by True (1910, pl. xx.). The outer border of the orbital plate of the frontal, as seen from above or below, is straighter than in *Berardius*. The amount of deficiency of bone in the antorbital tubercle is variable, to some extent probably depending on age. In one of the British skulls there is a large unossified cavity between the frontal and the maxilla in front and between the frontal and the malar and lachrymal below. This incompleteness probably represents a cartilaginous condition, mainly of the maxilla and malar, and in some cases it is much less marked than in the skull above indicated. The anterior lobe of the malar (*m*) is hatchet-shaped, its relation to the antorbital notch and tubercle being much as in *Berardius*. A part of its antero-external border appears on the outer side of the antorbital tubercle, immediately in front of the frontal and covered dorsally by the maxilla. The thickened border (*lt*) of the lachrymal does not nearly reach the outer edge of the antorbital region, and may be described as vestigial.

True's figures (1910, pls. xviii., xix.) indicate that the head of the malar of *Ziphius* may extend into the antorbital notch, Kernan (1918) has figured the isolated malar (pl. xxx. fig. 1) and lachrymal (fig. 2) of a young specimen.

\* The greater outward extension of the frontal is probably due to the fact that the surface formed by the thickened borders of the bones in question is not vertical, but faces obliquely outwards and ventrally.

† Threw of these are noticed on p. 154, Proc. Zool. Soc. 1918.

It should be noted that in this, as in the later diagrams, the internal edge of the lachrymal or malar, or of both these bones, is not indicated. This is because these bones are usually overlapped by slips of other bones, so that the real median edge is concealed. The lachrymal is typically overlapped by the palatine, and the malar by the maxilla.

*Hyperoodon rostratus* (text-fig. 1, c) has specially characteristic features in the orbital and antorbital bones. The outer border of the orbit is not so straight as in *Ziphius*, and becomes concave in old skulls, as seen from above or below. The antorbital tubercle is very large, and the antorbital notch is well developed. Largely owing to the great development of the maxillary crests on the dorsal side, the notch has a great vertical depth, its median boundary, formed principally by the maxilla with its crest, being a longitudinally vertical wall of considerable extent. The species is characterized by the great size of the malar and the reduction of the lachrymal. The anterior lobe of the malar, though varying in the proportionate size of its various parts, has the general shape of the head of a claw-hammer, as shown in the text-figure. Its antero-internal part appears in the figure as an acute triangle, which must be understood to form a considerable part of the vertical inner wall of the antorbital notch, and thus to extend along this wall in a direction at right angles to the plane of the drawing. In passing outwards the anterior lobe of the malar becomes greatly thickened, like the head of a hammer, and this part forms a variable proportion of the outer side, and even more of the anterior side, of the antorbital tubercle (otherwise constituted by the maxilla and frontal). In anterior and side views the arrangement is as in text-fig. 3, K, L, the antorbital tubercle being constituted above by the maxilla, the border of the malar appearing as a triangular lobe below it, and the strong frontal component appearing behind the malar (*cf.* Eschricht, 1869, pl. vi. fig. 1, skull of *H. latifrons* type).

One of the most striking features of *Hyperoodon* is the complete disappearance of the normal thickened border of the lachrymal (*l*), as shown in text-fig. 1, c, where the outer end of the bone appears to be pointed, a feature which is well shown on the right side of Eschricht's fig. 2. The apparent point is really the ventral end of a thin edge, which passes out of sight, between the frontal and the malar and runs obliquely dorsally and forwards. In a skull from Skegness (British Stranded Whales, 1913, No. 38) this edge reaches the dorsal surface, where it expands into a triangular portion, lying between the frontal and the malar. Although the lachrymal does not appear on the dorsal surface in most of the skulls I have examined, the Skegness skull is not altogether exceptional, as the same condition is figured by Eschricht in fig. 3 of the plate referred to above, and I have observed it in a skull in the collection of the Royal College of Surgeons. The figure given by Eschricht (1869, pl. vii. fig. 4) of the skeleton of a fetal *Hyperoodon* about 610 mm. long is of

special interest as showing the zygomatic portion of the malar as a bar extending continuously from the antorbital tubercle to the squamosal, along the inferior margin of the orbit, in a manner more nearly approaching that of the typical Mammalian malar than in the adult *Hyperoodon*.

Among the species of *Mesoplodon*, *M. layardi* most nearly approaches the preceding genera in the disproportionate size of the large maxillary and the small premaxillary foramina. This is of interest, since this species possesses a well-developed basi-rostral or upper dentary groove, a feature which may be regarded as primitive. The groove commences at the base of the rostrum, in a transversely elongated pit of the maxilla; and its commencement is visible in a ventral view of the skull (text-fig. 1, *d, b.g*). Although shallow, it is distinct along practically the whole length of the rostrum, being as much as 12 mm. wide opposite the front end of the external concavity of the pterygoid, then successively narrower, broader, and finally narrower again.

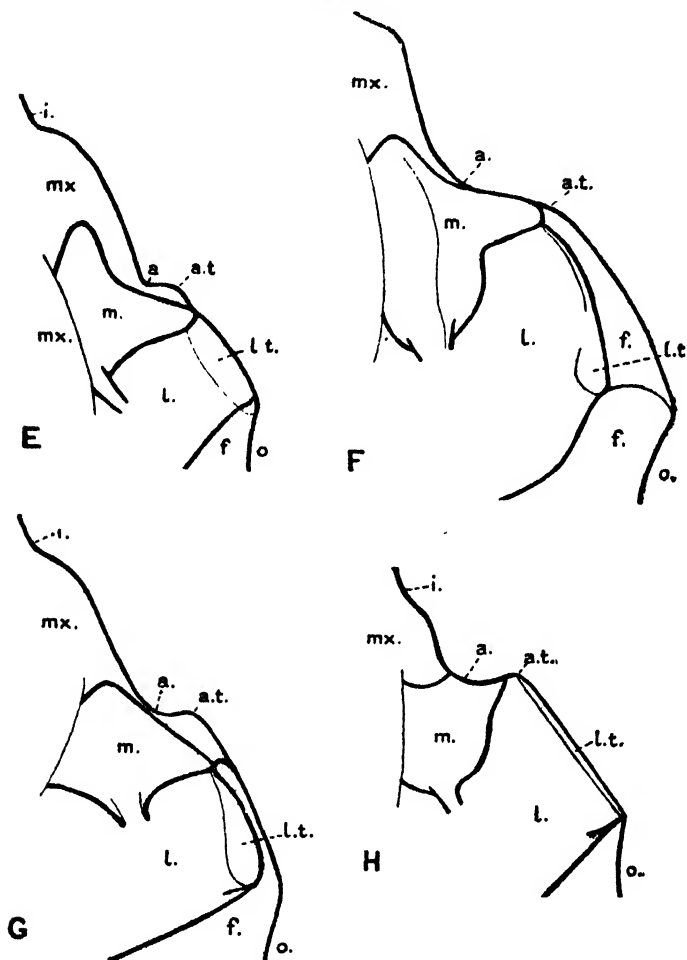
The antorbital region resembles that of *Berardius* in the fact that the surface formed by the thickened borders of the lachrymal (*l.t*) and frontal (*f.t*) is oblique, the outer border of the lachrymal thus not reaching the outer edge of the skull. In most species of *Mesoplodon* the junction of the outer part of the posterior edge of the lachrymal with the frontal is marked by a convexity which indicates the passage of the orbital into the antorbital region. In *M. layardi* the junction is unusually flat, both along most of the fronto-lachrymal suture and on the frontal, where there is no obvious separation of the orbit from the antorbital part. The posterior end of the thickened outer border of the lachrymal is, however, considerably raised, forming a distinct projection above the otherwise flat surface, extending into the anterior end of the orbit. The greater part of the antorbital tubercle is formed by the maxilla, and the malar only touches it on its inner side; with this exception not reaching any part of the antorbital notch. The malar appears unusual in shape, but its median portion is overlapped by the maxilla, and the shape of its antero-internal portion is thus not discoverable.

*M. grayi* (text-fig. 2, *e*) is the only other species of *Mesoplodon* having a well-developed basi-rostral groove, and it is here deeper than in the last species, and may be provided with a series of vestigial teeth towards the middle of the length of the rostrum, which has no lateral maxillary flanges at its base. The malar has a triangular antero-internal lobe, its external angle still reaching the outer side of the antorbital tubercle. The thickened border of the lachrymal faces mostly outwards, and completely reaches the outer edge of the antorbital region. It is not sharply raised posteriorly, where it forms a convexity passing gradually into that of the adjacent parts of the frontal. The appearance of the side view is described on p. 546.

*M. bidens* (text-fig. 2, *g*) agrees substantially with *M. grayi* in the relations of the antorbital bones, as seen in ventral and side

views. The thickened border (30–34 mm. long) of the lachrymal practically reaches the outer edge of the frontal, which is accordingly not or hardly visible in this region, in ventral view, in old

Text-figure 2.



Antorbital region (ventral view) of *Monoplodon*. E, *M. grayi*; F, *M. densirostris*; G, *M. bidens*; H, *M. hectori*. a, antorbital notch; a.t., antorbital tubercle; f, frontal; i, inner notch; l, lachrymal; l.t., thickened outer border of lachrymal; m, malar; mx, maxilla; o, orbit.

skulls. In a younger specimen (Rosslare) it is considerably overhung by the frontal. It is well raised and much thickened at its posterior end, corresponding with the anterior end of the orbit,



but not so abruptly as in *M. hectori*. The malar just reaches the outer edge of the antorbital tubercle, and it may touch the posterior part of the antorbital notch with its anterior border, although it is not visible in dorsal view. The tip of the antorbital tubercle is entirely formed by the maxilla.

In *M. stejnegeri*, so far as can be judged by the published figures, the side view (True, 1910, pl. ix. fig. 2) is as in the two preceding species, except that the thickened border of the lachrymal is thinner behind. The ventral view (True, pl. vi.) shows that the malar forms practically the entire boundary of the antorbital notch. This bone is apparently just visible in dorsal view (True, pl. iii.).

In *M. densirostris* (text-fig. 2, f; Pl. II. fig. 3) the lachrymal differs from that of other species in having lost the whole of its thickened outer border except a vestige (*lt*) at the posterior end, which is not definitely raised, the remainder of this border (the total length of which is 47 mm.) being very thin, apparently a characteristic feature of the species. The lachrymal is thus barely visible in a side view (Pl. III. fig. 5), but in True's figure (pl. vii. fig. 2) its thickened border is better developed than in the Porto Santo skull. The malar resembles that of *M. bidens* in general shape, but it forms the whole of the posterior border of the antorbital notch, and the whole of the ventral part of the front of the inconspicuous antorbital tubercle, with the exception of a small frontal component. An appreciable part of the bone appears, behind the notch, in the dorsal view of the skull (Pl. I. fig. 1).

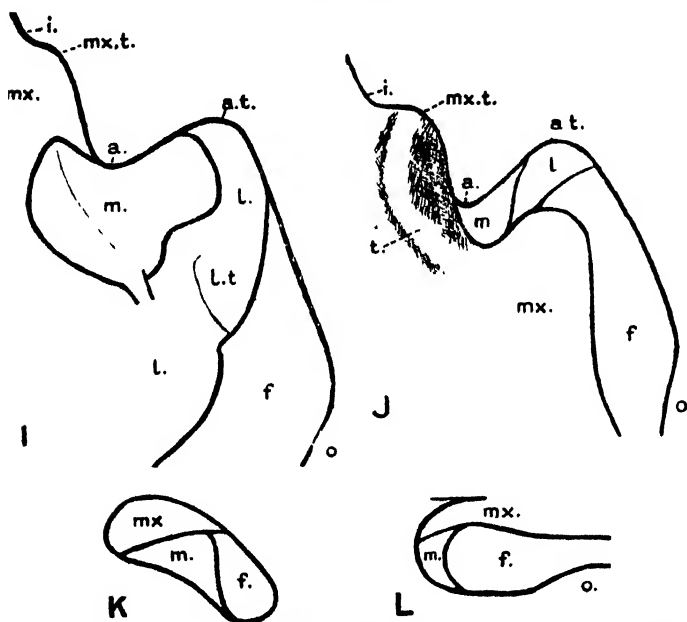
*M. mirus* (text-fig. 3, i; Pl. II. fig. 4) is peculiar, as has been pointed out by True (1913<sup>2</sup>, p. 653), in the construction of its antorbital tubercle, the greater part of which is formed by the lachrymal, which is best seen on the left side of Pl. II. fig. 4. In ventral view the thickened border of this bone forms the larger part of the tubercle, passing on the outer side of the malar, which is thus excluded from the lateral edge of the antorbital region. Its posterior end is hardly raised, and makes no projection into the orbit. The frontal extends on the outer side of the posterior half of the thickened border (50 mm. long) of the lachrymal, which in its anterior half forms the outer part of the tubercle, ventrally. The malar constitutes the entire posterior border of the antorbital notch, in this view. In dorsal view (text-fig. 3, j; Pl. I. fig. 2) a prolongation of the malar extends well on to the dorsal surface. The lachrymal continues its course round the tip of the antorbital tubercle, and ends in a point in front of the maxilla, here forming the lateral part of the antorbital tubercle. The maxillary tuberosities (text-fig. 3, j, t) are large and strong, with an oblique course.

The arrangements of these parts in *M. europæus* (Van Beneden and Gervais, pl. xxiv. fig. 1 b; True, 1910, pls. ii., v., viii.) appear to be not unlike those of *M. mirus*, but the inner notches and the anterior tubercles are less distinct, and the anterior extension of

the thickened border of the lachrymal is not so marked a feature. The well-developed maxillary tuberosities are straighter than in that species.

*M. hectori* (text-fig. 2, H) differs in several respects from the other species. While in other cases the thickened border of the lachrymal usually looks ventrally as well as outwards, thus being obvious in a ventral view, in *M. hectori* it faces completely outwards, reaching the outer edge of the skull along its whole course, without any separation from it by the frontal. Although

Text-figure 3.



Antorbital region of Ziphioids. I, *Mesoplodon mirus*, ventral view; J, *M. mirus*, dorsal view; K, *Hyperoodon rostratus*, anterior view; L, *Hyperoodon rostratus*, side view. a, antorbital notch; a.t, antorbital tubercle; f, frontal; i, inner notch; l, lachrymal; l.t, thickened outer border of lachrymal; m, malar; mx, maxilla; mx.t, maxillary tuberosity; o, orbit; t, maxillary tuberosity.

particularly thick and strong, its outward direction prevents more than its ventral edge being seen in a view from below. Its posterior end is abruptly raised, forming a distinct projection into the orbit (Flower, 1878, pl. lxxii. fig. 4). The external lobe of the anterior part of the malar is much reduced, and this bone is accordingly narrower than usual. It forms the posterior boundary of the antorbital notch, but it does not appear, or barely appears, in the dorsal view of the skull. Its zygomatic part (incomplete)

is conspicuously slender. On the dorsal surface the antorbital tubercle is formed entirely by the maxilla, the suture of which with the lachrymal passes horizontally through nearly the middle of the tubercle. In view of Oliver's association of this species with *M. mirus* in a distinct genus, *Puikaea*, it is of interest to notice that the two species do not resemble one another in the characters of their antorbital regions.

It follows from what has already been said that the malar shows considerable differences in the members of the Ziphioid group. It is probably a safe assumption that in the ancestors of the Cetacea this bone reached the outer surface of the skull, and had the relations of the typical Mammalian malar, which takes part in the formation of the zygomatic arch by forming a bridge between the maxilla and the squamosal. The genus of existing Cetacea which best shows this relation is *Physeter*, where the malar is a thick and heavy bone protecting the orbit below and reaching the maxilla and squamosal at its two ends. No distinct lachrymal is present, but as pointed out by Flower (1868, p. 319), it gives off a process which is wedged in between the under surfaces of the orbital plates of the maxilla and frontal. In *Kogia* (Miller, 1923, p. 45, pl. vii. fig. 3) this process is a conspicuous feature of the lateral view of the skull, but the zygomatic process does not extend beyond the anterior end of the orbit, and is widely separated from the squamosal. In the *Mystacoceti* the malar forms a well-developed and complete zygomatic arch, but these whales are usually described as possessing a distinct lachrymal, in the form of a thin slip of bone wedged in obliquely between the maxilla and the frontal (Eschricht, 1869, pl. i. fig. 1). This appears to correspond with the ascending process of *Physeter* and *Kogia*, and it has the same relations to the maxilla and frontal. It is wanting in most of the skulls I have examined, but in an articulated skeleton of *Neobalaena* (on the left side) the anterior end of the malar is continuous with a slip of bone having the relation of the lachrymal to the maxilla and frontal ordinarily described in *Mystacoceti*. I have found a similar extension of the malar on both sides in an articulated young Welsh specimen of *Balaenoptera physalus*, also in the British Museum.

In the *Delphinidae*, as in *Physeter* and *Kogia*, no distinct lachrymal is present, but part of the malar corresponds exactly in position with the lachrymal of *Ziphiidae*, in partial accordance with Flower's conclusion (1872, p. 204) that the distinct lachrymal in this family is to be regarded as a bone segmented off from the posterior part of the malar. There is probably more to be said for the opposite view, that the lachrymal and malar have fused in the *Delphinidae*. In a side view, the antorbital region of an ordinary Dolphin may be seen to be constituted mainly by the maxilla, dorsally, while the ventral part may consist entirely of the oblique thickened border of the undivided malar, which is

overlapped dorsally by the frontal to an extent varying with the species (cf. Miller, 1920, Proc. U.S. Nat. Mus. lvii. pl. xxix.). The arrangement is in fact almost the same as in *Mesoplodon hectori*, as shown by Flower (1878, pl. lxxii. fig. 4), except that the lachrymal element is not distinct. The relations of the malar in Delphinidae would be represented by the removal, in text-fig. 1, A (*Berardius*), of the curved suture between *lt* and the zygomatic process of the malar, and by prolonging the outer border of the lachrymal component as far outwards as that of the malar component. In some of the ordinary Dolphins the malar-lachrymal not only forms the whole of the ventral surface of the antorbital tubercle, but it is prolonged round its front end to its dorsal side to a larger or smaller extent. In the typical Dolphins the bone in question generally bounds the antorbital notch posteriorly, being developed principally on its outer side, a smaller extension passing forwards along the inner margin of the notch, and this is also the case in *Monodon* and *Delphinapterus*. Among the freshwater Dolphins, in *Lipotes* (Miller, 1918, Smithsonian. Misc. Contr. lxviii. No. 9, pls. ii., iv., vi.), the same bone extends largely on to the dorsal side of the antorbital tubercle, and forms the whole of its anterior part on the ventral side as well (confirmed by a skull in the British Museum). In *Inia* I find that it is much smaller, and in *Platanista* that it is vestigial. Among the Ziphioids (text-fig. 1, A-C) *Berardius*, *Ziphius*, and *Hyperoodon* show what may be regarded as the primitive arrangement, in the extension of the malar to the outer border of the antorbital region. This condition persists in certain species of *Mesoplodon*, but in others, and notably in *M. mirus*, the lachrymal excludes the malar from that border.

It appears to me that the comparative study of individual bones in the Cetacean skull may yield more important results than the mere recording of measurements; and the antorbital region seems to offer a specially promising field for further observations. The examination of young, and probably of fetal skulls may be necessary, in order to establish satisfactorily the homologies of the malar-lachrymal complex in various members of the group.

#### *On the genus Paikea.*

In 1922 Oliver (1922, p. 574) proposed the genus *Paikea* for Ziphioid Whales "with the cranial characters of *Mesoplodon* and two terminal teeth in the lower jaw." The genotype is *Berardius hectori* Gray, 1871 (= *Mesoplodon hectori* Flower, 1878), and the genus included *Mesoplodon mirus* True, 1913. The presence of two well-developed teeth at the anterior end of the mandible is undoubtedly a striking difference from other species of *Mesoplodon*, in which the two teeth are in the neighbourhood of the posterior end of the symphysis. I have previously suggested (1919, p. 21) that in *M. mirus*, as in *Ziphius* and *Hyperoodon*, these teeth represent the anterior pair of the four found in

*Berardius*, while the teeth of other species of *Mesoplodon* correspond with the posterior pair of the same genus.

Abel (1905<sup>2</sup>, pp. 40, 88), discussing the palæontological evidence bearing on the ancestry of the Ziphiidæ, derives these animals from ancestors with a series of functional teeth in both jaws and a long mandibular symphysis. The evolution of the family has resulted in the suppression of the maxillary teeth, except for the vestigial teeth which occur not infrequently, in the shortening of the symphysis of the mandible, and in the reduction of the lower teeth to one or two pairs. In *Palæoziphius* (figured by him on p. 91) the lower jaw (Upper Miocene) shows a series of well-developed alveoli, of which the first and seventh pairs are somewhat enlarged\*. In *Cetorhynchus* (p. 94), also from the Miocene, the lower teeth are shown to be in process of reduction by the breaking down of the bony septa present in *Palæoziphius* between the alveoli; while the upper jaw of *C. christoli* is provided with about 40 alveoli, pointing to a total number of 50-55 pairs of teeth. *Mioziphius*, of the Upper Miocene, is characterized by Abel (p. 101) as possessing 37-48 maxillary alveoli, of which the septa have broken down, giving rise to a broad and shallow dentary groove. The mandible has a symphysis which is shortened as compared with that of the two preceding genera. Its dentary groove is reduced posteriorly, but near its anterior end it bears two projecting sockets on each side (fig. on p. 103), implying the presence of two pairs of teeth very similar to those of the recent *Berardius*. In *Anoploussa* also (figured by True, 1907, pl. ii.) the mandible bears two pairs of large teeth, the posterior teeth 47 mm. behind the anterior pair, with which they are connected by a dentary groove, in the floor of which are several foramina, perhaps representing vestigial teeth.

From the evidence of these fossils, reinforced by that of *Berardius*, it appears that, in certain genera at least, the reduction and disappearance of most of the mandibular teeth took place simultaneously with the persistence of two pairs of teeth at the front end of the jaw; and that at a later stage in evolution one of these two pairs also disappeared. It does not necessarily follow that the vanished teeth are the same pair in all cases. Oliver (1922, p. 575) refers to a skull of *Berardius arnuxii*, in the Wellington Museum, New Zealand, in which the anterior pair of teeth are alone present. In *Hyperoodon*, often described as having the anterior pair only, a smaller tooth may occur behind each tooth of the normal pair. I venture to suggest that *Mesoplodon* has remained in a plastic condition in this respect, and that, having retained a latent capacity to develop a single member of a series of tooth-germs, on either side, into a functional tooth, there is some latitude as to the one actually selected for this purpose. The anterior tooth becomes functional in *M. mirus* and

\* It should be noted that True (1907, p. 105) is not satisfied that *Palæoziphius* is a Ziphioid; and Winge (1921, p. 92) has criticisms to the same effect.

*M. hectori*, and a more posterior tooth, perhaps not necessarily occupying the same position in the series in all cases, in the other known species of the genus. Such instances as that of *M. densirostris* (Pl. IV. fig. 8), in which there is an elongated dentary groove ending with the functional tooth, raise a doubt as to the exact homology of this tooth. Unless translation from one part of the jaw to another has occurred, it seems probable that it corresponds with a later member of the series, rather than with the second tooth of *Berardius*. Embryological evidence may prove capable of throwing light on this point. Owen (1870-1889, p. 31) clearly stated the view that the functional teeth of Ziphioid Whales are not the same members of the series in all cases. He considered that, in view of the frequent occurrence of vestigial teeth in the alveolar groove, it is a matter of slight morphological importance which of them become well developed. Without following him in his conclusion that *Berardius*, *Ziphius*, and *Mesoplodon* are not generically separable, a view which appears to me to be negatived by the cranial characters, I can at least accept his general point of view to the extent of believing that the position of the mandibular teeth does not necessitate the removal of *M. mirus* and *M. hectori* from *Mesoplodon*.

If it were justifiable to separate two of the species of *Mesoplodon* as a distinct genus, on the evidence of the mandibular teeth, it ought to be possible to point to other characters in support of this conclusion. In introducing the genus *Paikea*, Oliver admitted that it had the cranial characters of *Mesoplodon*. The only features which he claims to exist in common in *M. mirus* and *M. hectori* are the broad and deep rostrum, the long mandibular symphysis, and the facts that the dorsal fin is placed far back and that the teeth are completely covered by the gums. The last statement is correct for the female specimen of *M. mirus* described by True, but it applies equally to the females of other species of *Mesoplodon*. It is not correct for the male from Liscannor, which agreed with the males of other species in having large teeth projecting beyond the gums. The rostrum of the species referred by Oliver to *Paikea* is not broader than that of *M. europæus*, nor so deep as that of *M. densirostris*; and the position of the dorsal fin does not appear to differ materially in position from that of other species of *Mesoplodon*.

My principal reasons for not accepting *Paikea* are (1) that, with the exception of the position of the teeth, *M. mirus* and *M. hectori* possess no single character in common which justifies their close association with one another or their separation from other species of *Mesoplodon*; (2) that in its cranial characters generally *M. mirus* resembles *M. europæus* so closely that it is hardly possible to place them in different genera; (3) that if it were proposed to enlarge *Paikea* by the inclusion of *M. europæus*, the principal generic character would disappear, since the teeth of *M. europæus* are in the neighbourhood of the posterior end of the

symphysis, as in most of the other species of *Mesoplodon*. The cranial characters of *M. hectori* are compared below (p. 567) with those of *M. mirus*.

**MESOPLODON MIRUS** True. (Plates I. IV. figs. 2, 4, 6, 7, 9; text-fig. 3, p. 553, i, j.)

*Mesoplodon hectori* Anderson, 1901, p. 117, text-figs. 1-3 (skull).

" " (*pars*), Anderson, 1905, p. 703.

(Species not mentioned), Anderson, 1902, p. 1121, text-fig. 14, 1, 2 and 3 (skull).

*Mesoplodon mirum* True, 1913<sup>1</sup>, p. 1; 1913<sup>2</sup>, p. 651, pls. lii.-lvii. (external features, skull, lower jaw).

*Ziphius cavirostris* Harmer, 1918, pp. 5, 8, 18.

*Mesoplodon mirus* Harmer, 1919, pp. 3, 5, 18, text-fig. 2 (lower jaw).

*Mesoplodon mirum* Oliver, 1922, p. 574 (referred to *Paikaea*, n. gen.).

In 1901 Prof. R. J. Anderson gave a short account, with poor figures, of a skeleton of a Beaked Whale, the sex of which was not recorded, in the Museum of Queen's College, Galway. On account of the presence of a tooth on each side of the apex of the mandible the specimen was referred to *M. hectori* (Gray). In a later paper (1905) he stated that the specimen was a young one, 4.25 metres (nearly 14 feet) long, which was stranded near Galway, "some years ago." He described at the same time a larger specimen, 6.37 metres (20 feet, 10½ inches) long, also referred to *M. hectori*, which had been stranded on one of the Aran Islands, Galway Bay, in the winter of 1903/4, also recorded by him in another paper (1904, p. 126). I have previously pointed out (1919, p. 20) that Anderson's larger specimen, from the Aran Islands, belongs to *Ziphius cavirostris*.

True's account of *M. mirus* was based on photographs of the external appearance and on the head, tail, and one flipper, received at the U.S. National Museum, of an adult female, 16 feet long, which had been stranded on the outer bank of Bird Island Shoal in Beaufort Harbor, North Carolina, on June 26, 1912. The description of its colour is as follows:—"Back, slate-black; lower sides, yellow-purple, flecked with black; median line of belly somewhat darker, a grayish area in front of vent; fins the color of the back." True showed conclusively that *M. mirus* is easily distinguishable, in size and cranial characters, from *M. hectori*. The teeth were about 30 mm. long and their greatest diameter about 9 mm. In Anderson's specimen the right tooth, now lost, was one inch (25 mm.) long and three-eighths of an inch (11 mm.) wide (1901, p. 117); pointing to the conclusion that, like the one recorded by True, it was a female.

The specimen (Brit. Mus. 1920, 5.20.1) specially described in this paper was found alive at Liscannor, Co. Clare, on June 9, 1917, and was driven ashore by fishermen in boats. It was

stated to have been 17 feet in length and 9 feet in girth, the whole of the head and the dorsal side of the body being black, the lower surface of the head being of a very light colour, "approaching white," without any other markings. As the cranial measurements are slightly larger than those recorded by True, the recorded lengths of the animals confirm one another. The two descriptions of the colour do not altogether agree. As soon as possible after the receipt of the news of the stranding of this specimen, Mr. T. Gerrard went to Liscannor, on behalf of the British Museum, to secure the skeleton, but he found on arrival that the blubber had been completely removed and boiled down, and it was thus impossible to obtain further information about the external characters. The right flipper had been lost, but nearly the whole of the rest of the skeleton was secured, as well as the penis, which placed the sex beyond doubt. The animal was wrongly recorded as *Ziphius cavirostris* in my 5th Report (1918) on Cetacea stranded in 1917. In the Report (1919) for the following year I acknowledged the services of the late Mr. W. Taylor in suggesting that the specimen might prove to belong to True's Beaked Whale, and the kind assistance which had been given me by Prof. J. Mangan in sending measurements and sketches of the two Ziphioids in the Galway Museum.

In 1922 Oliver referred the present species to his new genus *Paikea*, of which *Mesoplodon hectori* is the type.

The species is thus known by three specimens, two of which are known to be respectively male and female, while the Galway individual was probably a female. True (1913<sup>2</sup>, p. 652) quotes Mr. Lewis Radcliffe, Director of the Fisheries Laboratory at Beaufort, who believes that *M. mirus* is not uncommon in that neighbourhood. This suggests that the natural habitat of the species is the Gulf Stream, an idea which appears to be confirmed by the occurrence of two specimens on the West coast of Ireland.

### *Skull.*

The cranial characters of the Liscannor specimen agree closely with True's account of the type-specimen, and with those of the Galway individual, as described by Anderson and in Prof. Mangan's letters to me. The presence of teeth at the extreme front end of the lower jaw distinguish it at once from all other species except *M. hectori*, in which the cranial characters are very different, as shown, for instance, by the form of the rostrum and of the vertex of the skull, and by the shape of the lower jaw. In the table which follows I have used the measurements given by True; and as the Liscannor skull is practically identical in length with the type-specimen, the comparison of the two is easy. I have reproduced True's measurements, and I have added those which I am able to give of the Galway specimen, on the authority of Anderson and Mangan. I have also included, for comparison,



*Mesoplodon*. Cranial measurements, in millimetres.

	E = estimated.	<i>M. miras</i> , ♀ Type (True).	<i>M. miras</i> , ♂ Brit. Mus. Liscannor.	<i>M. miras</i> (probably ♀) Galway Mus.	<i>M. aetforti</i> Type Brit. Mus.	<i>M. densirostris</i> (probably ♂) Brit. Mus. Porto Santo.
A	Skull, total length .....	810	814	782, E.	587, E.	765, E.
B	Skull, height, vertex to inferior borders of pterygoids.....	301	315	273	235	302
C	Skull, width at centre of orbits...	325	337	—	228	306
D	Skull, width across zygomatic processes .....	345	356	330	258	306
E	Tip of rostrum to post. border of pterygoids, near middle line ..	618	630	—	443, E.	620
F	Width across occipital condyles ..	125	117	—	90	—
G	Rostrum, length, from level of bases of antorbital notches .....	496	520	485, E.	343	490
H	Rostrum, width, between bases of antorbital notches... ..	210	200	—	137	185
I	Rostrum, width, between bases of inner notches .....	—	150	146	104	96
J	Rostrum, width, at middle .....	60	67	--	37	61
K	Premaxillæ (both), width across expanded proximal ends .....	142	165	150	—	121
L	Premaxillæ (both), width (least) opposite anterior nares ..	118	120	—	104	104
M	Premaxillæ (both), width opposite premaxillary foramina ..	68	75	—	67	65
N	Anterior nares, greatest width .....	56	59	—	40	47
O	Maxillary foramina, least distance between .....	92	91	—	79	65
P	Maxillary foramina, post. border of, to end of maxillary tubercle .....	63	61	—	38	61
Q	Vomer, as visible on palate, greatest length .....	162	135	—	89	—
R	Mandible, length of ramus, to end of condyle .....	668	700	610	481	680
S	Mandible, length of symphysis.....	193	190	152	155	195
T	Mandible, greatest height at coronoid process .....	117	122	114	83	130

measurements of the type-specimen (Brit. Mus. 16776-76.2.16.3) of *M. hectori*, as well as of the Porto Santo *M. densirostris* described in a later section of this paper. The characters which appear to be specially distinctive of *M. mirus* are the position of the teeth, the massive character of the lower jaw in the region of the symphysis, the proportions of the rostrum, the large size of the antorbital notches and of the maxillary tuberosities, the characters of the lachrymals and nasals, and the form of the vertex of the skull, particularly the vertical position of the postero-internal ends of the maxillæ. In view of the rarity of the species I subjoin further details of the skull and of the skeleton, which has not previously been described.

*Dorsal view* (Pl. I. fig. 2).—The mesorostral is well ossified throughout, to a point only a few millimetres from the tip. In this respect it contrasts strongly with two skulls of *M. bidens* in the British Museum. Both are apparently adult, and while one of them (Fraserburgh, Aberdeenshire. 8.2.28.1) is known to be male, the other (Skegness, Lincs, 1920.12.20.1) is probably female, from the characters of its teeth. In these skulls the mesorostral ends in an acute point about 170 mm. from the tip of the rostrum (which is, however, not quite complete at that end in either skull), and this point corresponds exactly with the anterior termination of the vomer. While in *M. mirus* the surface of the ossified mesorostral rises almost to the level, but at no point surpassing that level, of the premaxillæ along its whole length, both skulls of *M. bidens* show a large depression of its surface at the posterior end, the floor sloping obliquely upward along the premaxillæ at the two sides. In the male *M. bidens* the mesethmoid is considerably thickened, dorsally, for nearly 30 mm. in front of the premaxillary foramina, ending abruptly in front with a truncate edge, 17 mm. wide, the posterior part of the ossified mesorostral lying at a much deeper level. In *M. mirus* (male) the mesethmoid is ossified in the same way, but although its junction with the mesorostral is indicated, the dorsal surfaces of the two bones are continuous and at the same level. In True's female skull the mesorostral is much less ossified, and it is distinctly depressed in front of the mesethmoid. The rostrum is bifurcated at the tip, as shown by True's figures, the mesorostral ending 13 mm. from the end, and the relations of the dorsal edges of the premaxillæ correspond with his description. At the base of the rostrum they have their inner edges not much raised above the outer edges. Further forward the slope becomes much steeper, and in front their dorsal surfaces are almost vertical. At 350 mm. from the tip the inner or upper edge of the premaxilla is 25 mm. above the lateral maxillary flange. At the level of the premaxillary foramina, which are slightly in advance of the maxillary foramina, the premaxillæ are 13 mm. apart (15 mm. just behind this point), thence converging forwards, and approaching one another within 3 mm. at a point

200 mm.\* from the tip of the rostrum, again diverging to a distance of 11 mm. at the tip.

The thickened mesethmoid diminishes in width backwards to the anterior border of the nares, where it is 5 mm. wide. Here the edge of the nasal septum becomes thin, and descends vertically, forming a deep sinus, the posterior border of which ascends, nearly vertically, to a higher level, and forms a thickened surface in contact with the suture of the nasals.

The base of the rostrum is indicated by the antorbital notches, which are conspicuous in this species. These are bounded externally by the antorbital tubercle and on the inner side by the maxillary tubercle, in which ends the relatively large maxillary tuberosity, running obliquely forwards and outwards and with a length of about 50 mm., the left slightly the larger in the *Liscannor* skull. On the median or inner side of the maxillary tubercle is a smaller emargination, the inner notch. This region of the skull has a special similarity to the same part in *M. europæus*, as has been pointed out by True. The rostrum is 200 mm. wide at the antorbital notches and 150 mm. at the inner notches. It is bordered, on each side, by a thin lateral flange, commencing at the maxillary tubercle, where it is at its widest, and diminishing in width as it passes forwards. By comparison with *M. grayi* and *M. layardi* it appears that the basi-rostral groove characteristic of those species is in some way represented by this flange, which corresponds either with the dorsal ridge of the basirostral groove or has perhaps been formed by the coalescence of the dorsal and ventral edges, on the disappearance of the groove. The latter conclusion is suggested by comparison with *M. layardi*, in which the ventral end of the groove passes into the maxillary tubercle. At their commencement the lateral flanges are concave dorsally, as in other species, but their outer edges are so much raised in the *Liscannor* skull that a line joining their posterior ends passes completely above the level of the premaxillæ. This condition lasts for about 20 mm., after which the premaxillæ rise above the level of the flanges, a relation which is found along the whole length of the rostrum in *M. bidens*. At their origin (*M. mirus*) the flanges are 50 and 45 mm. wide (R, L). They descend gradually along the sides of the rostrum (Pl. III. fig. 6), and at about 180 mm. from its tip they have reached its ventral surface. At about 230 mm. from the tip the ridge is seen to commence to open out into a narrow groove (as shown in True's pl. lvi.), at first only one or two mm. wide, but further forward becoming an obvious dentary groove, which passes beyond the maxillæ, which end 55 mm. from the tip of the rostrum, on to the premaxillæ.

Between the premaxillary foramina (Pl. I. fig. 2) and the anterior nares the premaxillæ widen out into expanded portions,

\* The position of points measured from the tip of the rostrum can be ascertained by the eight paper-marks seen in Pl. I. fig. 2, placed at uniform distances of 80 mm apart.

which are concave or spoon-shaped dorsally. The width of the bones is here 61 and 44 mm. (R, L), while at the narrow portion, opposite the nares, the respective least widths are 36 and 27 mm. Behind the nares the expanded posterior ends of the premaxillæ are revolute and of large size. At the level of the expanded part of the mesethmoid in contact with the nasals the premaxillæ are respectively 77 and 52 mm. wide (R, L), and there is a corresponding predominance in size, as well as in extent of revolution, in the expanded dorsal end of the right premaxilla over that of the left side.

The vertex of *M. mirus* is greatly elevated, and in such a way that the posterior parts of the maxillæ are vertical in position, where their thickened edges appear at the sides of the vertex and behind the expanded crests of the premaxillæ. In a dorsal view of the skull the posterior ends of the maxillæ show only their edges, but in *M. bidens* they slope upwards and inwards towards one another. In side view, as shown in True's pl. lvi., the outer edge of the maxilla passes from the posterior end of the orbit in a continuous curve until the maxilla assumes a vertical position, where there is a slight indentation of its outline, partially separating an ear-like dorsal region, which is a noteworthy feature of the Liscannor skull (Pl. III. fig. 6). In order to indicate the dimensions of the frontal plates of the maxillæ I give the following measurements, including the corresponding measurements of *M. densirostris*, which are required in connexion with the description of its skull:—

	<i>M. mirus.</i>	<i>M. densirostris.</i>
Ant. end of max. tubercle to post. end of maxilla . . . . .	245	240
Edge of max. at middle of orbit to its most dorsal part at vertex . . . . .	197	210
Width of maxilla at middle of orbit . . . . .	103	105
Width of frontal uncovered by maxilla at same point . . . . .	11	4
Longitudinal diam. of dorsal end of max., behind premax. crest . . . . .	70, 80 (R, L)	54
Least width of vertex, between maxillæ . . . . .	70	(incomplete)

In addition to the maxillæ and the premaxillæ the frontals and the nasals take part in the formation of the vertex of the skull. There is a small area behind the nasals where the frontals are exposed, the left one rather the larger in the Liscannor skull, so that the frontal suture lies mostly on the right of the middle line.

The nasals have a very characteristic shape. The two together measure 42 mm. across in front and 50 mm. behind. Individually (R, L) they are 27, 16 mm. in transverse diameter at the middle. Each has a distinct outer lobe, that of the R. nasal 56 mm. long, which takes part in the formation of the most prominent part of the vertex, forming the commencements of the revolute crests belonging to the premaxillæ. In the case of the R. nasal the outer lobe is broader than the inner lobe and is separated by a

sigmoid suture from the premaxilla. In the *L. nasal* the two lobes are of equal width, and its suture with the premaxilla is straight and longitudinal. The inner lobes are much below the surface of the others, and their anterior surfaces curve over to assume a vertical position in front, thus forming the posterior walls of the narial passages. A precisely similar conformation of the nasals is shown in an excellent drawing by Prof. Mangan of the Galway skull, and can be recognized in True's figure (pl. liv.) of the Beaufort skull. True's figures (1910, pl. ii.) seem to indicate a similar arrangement in *M. europæus*. In *Hyperoodon* I find that both nasals participate in the formation of the crests constituted mainly by the premaxillæ. In *Mesoplodon layardi* the *R. nasal* has this relation, but there is no marked distinction between inner and outer lobes. On the left side, in the same species, the region of the outer lobe is vestigial and does not nearly reach the summit of the crest. In *M. bidens* the outer lobes of both nasals are vestigial and not concerned in the formation of the crests.

The supraoccipital is 203 mm. across between the posterior ends of the temporal fosse, and its surface is gently convex.

The skull as seen in lateral view is figured by True (1913<sup>2</sup>, pl. lvi.), and the Liscannor skull (Pl. III. fig. 6) closely resembles that specimen. The malar is not visible in side view, being concealed by the antorbital tubercle. The thickened edge of the lachrymal is overhung by the frontal, but it can be seen, rather in the background, on the antero-ventral side of the antorbital part of that bone, curving up in a characteristic way in front to form a considerable part of the antorbital tubercle. The temporal fossa is conspicuously high as compared with other species. It measures 85 mm. in greatest vertical height, and its length from behind to its pointed front end is 122 mm. On the ventral side of the temporal fossa the outer side of the squamosal is marked by a deep oval depression, 46 mm. long and 23 mm. wide, which can be recognized in True's figure; and the same bone bears a longer, narrower, groove, mostly behind and on the ventral side of the first one, from which it is separated by a distinct ridge. The pterygoid is as shown by True, with a comparatively narrow notch behind, its outer concavity subdivided into three parts at its ventral end, of which the third is the deepest. The posterior borders of the pterygoids, near their median suture, are transverse. Beneath the antorbital notch the palatine is a strip, 28 mm. wide, on the dorsal side of the pterygoid, but at the front end of the pterygoid this part of the palatine is only 5 mm. wide, corresponding closely with True's figure (pl. lvi.).

In ventral view (Pl. II. fig. 4; True, pl. lv.) the *L. palatine* projects forward to a point situated 23 mm. in front of the pterygoid, the *R.* not quite so far. Each sends a narrow strip round the front end of the pterygoid to its inner side, and these are separated by parts of the maxillæ, together about 11 mm. wide. The maxillæ are visible further back than the palatines.

The proportions of the rostrum are indicated by the following table, which gives the height of the rostrum measured in the middle line, with the greatest width at the same level, at a series of points (shown in Pl. I. fig. 2) 60 mm. apart in the length of the rostrum. Comparison with the same measurements of *M. densirostris* given on p. 580 will show the striking difference between the two species, the height being greater than the width in all parts except the extreme tip in *M. densirostris*, and much less than the width in *M. mirus*.

	Distance from. tip of rostrum.	Height.	Width.
A .....	60	22	31
B .....	120	30	41
C .....	180	34	50
D .....	240	40	65
E .....	300	45	76
F .....	360	51	89
G .....	420	58	106
H .....	480	69	145

The great width in the proximal parts of the rostrum of *M. mirus* is due to the large development of the maxillary flanges. The measurement H is practically the width of the rostrum at the inner notches, as it is only 8 mm. in advance of that point.

The peculiarities of the antorbital region have already been described (p. 552).

The large basioccipital ridges of the ventral side differ in the skulls in which I have compared them. In *M. mirus* they are much sloped outwards (Pl. II. fig. 4 and True, 1913<sup>2</sup>, pl. lv.), their posterior halves are subparallel, and their inner surfaces have a concavity continuous with that of the median region of the skull. The anterior halves are strongly convergent, and pass continuously into the parts of the pterygoids lying above the pterygoid notches. In *M. hectori* the ridges are much more erect, their convergence towards the middle line is uniform along their whole length and not very great, and their inner surfaces are flat or very slightly convex. The connexion between the ridge and the pterygoid is interrupted. In *M. bidens* the slope and convergence of the ridges are as in *M. mirus*, but the inner surface is flat or slightly concave at the middle. The connexion between the ridge and the pterygoid is interrupted. In *M. densirostris* (Pl. II. fig. 3) the ridges are practically straight and converge but little, their inner surfaces slightly concave at the middle, and the connexion of their anterior ends with the pterygoids continuous. Owing to their position, which is more vertical than in the other species, the space between them is specially wide and deep, and it is not specially contracted in front as in *M. mirus* and *M. bidens*, and to a less extent in *M. hectori*.

The transverse diameter of the presphenoid, at the junction of

the basiooccipital ridges with the pterygoids, is noticeably smaller in *M. hectori* and *M. densirostris* than in the other two species.

Another feature in which *M. mirus* differs from the same three species is the massive character of the zygomatic process of the squamosal, which is truncate at its anterior end (Pl. II. fig. 4), where it meets the frontal, and is here 42 mm. across. In the other species (Pl. II. fig. 3) it is more rounded in front, and in none of them does its front end approach the size of the same structure in *M. mirus*, in which moreover the glenoid cavity occupies a smaller proportion of the ventral side of the bone, the concavity on the median side of the articulation being wider than in the other species.

On the palatal surface (*M. mirus*) the vomer becomes visible at 177 mm. from the tip of the rostrum, and is exposed for 132 mm. During most of its course it stands up as a high, narrow ridge, bordered by a longitudinal groove on each side. In front of the vomer is a median suture between the two premaxillæ, and the median part of the palate is here a longitudinal ridge, wider and less definite than that of the vomer, and bordered by longitudinal grooves continuous with those at the sides of the vomer. At 225 mm. from the tip of the rostrum is a palatal foramen, from which a groove runs obliquely forwards to join the groove at the side of the vomer, near the anterior end of the exposed surface of this bone. At the level of these foramina the rostrum is 59 mm. wide and 38 mm. deep in the middle line. Further back, at the level of the front ends of the palatines, it is gently convex, without grooves, and is here 104 mm. wide and 58 mm. deep.

Judging by its cranial characters *M. mirus* comes nearer to *M. europæus*, as described by Van Beneden and Gervais (1868-1879, p. 404, pl. xxiv.) and True (1910, p. 11, pls. ii., v., viii.) than to any other member of the genus; a conclusion already stated by True (1913<sup>4</sup>). The two species resemble one another in the shape of the base of the rostrum, with its well-developed lateral maxillary flanges, in the conspicuous maxillary tuberosities and antorbital notches, in the expanded, revolute, proximal ends of the premaxillæ, in the form of the nasals, and in the nearly vertical position of the posterior ends of the maxillæ. True (1913<sup>2</sup>) has called attention to the straighter lateral outline of the rostrum in *M. mirus* (convex near the middle in *M. europæus*), the more oblique maxillary tuberosities of the former, the peculiarities of the lachrymal, and certain other differences. The principal distinguishing feature is the position of the teeth, which in *M. europæus* are situated slightly in advance of the posterior end of the short symphysis.

I have indicated above (p. 557) my reasons for not accepting the union of the two species having the teeth at the anterior end of the mandible in the genus *Paikea* Oliver. The only known specimen of *M. hectori* is the type-skull described by Flower (1878, pl. lxxi. fig. 4; pl. lxxii. fig. 4); and as this is in the

British Museum, I am able to add the following notes with regard to its differences, in cranial characters, from *M. mirus*:—Its cranial portion is relatively much longer than that of *M. mirus*, and its rostrum is correspondingly shorter. The basal section of the rostrum is elongated, resembling that of *M. stejnegeri* (True, 1910, pl. iii. fig. 2) or *M. grayi* (Flower, 1878, pl. lxxi. figs. 1-3) more closely than that of *M. mirus*. The maxillary tuberosities and lateral flanges of the rostrum are only slightly developed. The premaxillæ are much broader relatively than those of *M. mirus*, opposite the anterior nares, and their proximal ends are not revolute. The maxillæ are not nearly so vertical at their posterior ends, and the temporal fossa is much lower. I have called attention above to differences between the two species in the characters of their antorbital regions (pp. 552-554) and of their basioccipital ridges (p. 565). A special peculiarity of the skull of *M. hectori* is that the thin part of the mesethmoid forming the nasal septum has no dorsal sinus and rises as a curved, slightly convex border above the level of the premaxillæ in the region of the anterior nares. Other differences between the two species are to be found in the mandible, as described below. I am completely in agreement with True's statement (1913<sup>2</sup>, p. 657) that the skull of *M. hectori* "presents quite different characters from that of *mirum*."

*Mandible* (Pl. III. fig. 6, Pl. IV. fig. 9).—The three specimens of *M. mirus* agree closely, as indicated by the comparison of the Liscannor jaw with True's account (1913<sup>2</sup>) of the Beaufort individual and with Prof. Mangan's sketches of the Galway animal. The very straight external border of the front part is a conspicuous feature. The symphysis\* is relatively longer than in *M. europæus* (True, 1910, pl. xi. fig. 6), and hardly shorter than in *M. bidens*. The apex of the Liscannor mandible is broad (44 mm.) and truncate, the jaw reaching a transverse diameter of 78 mm. opposite the posterior end of the symphysis. The teeth are at the extreme anterior end, those of the Liscannor specimen (male) measuring 26 mm. in diameter, longitudinally, at the summit of the alveolus, and 14 mm. transversely. They are thus strongly compressed, a character noted by True in his female specimen, in which, as in the Galway individual (probably also a female), the teeth are much smaller, with a transverse diameter of 9 to 11 mm. The free ends of the teeth of the Liscannor mandible were unfortunately cut off by the finders, and their length cannot be stated with accuracy. Their greatest projection from the alveoli, from which they have not been removed, is at present 23 mm.

The dentary groove is indicated by a row of small foramina, and it follows a remarkably straight course from the tooth to the

\* The length of the symphysis is best measured to the point on either side corresponding with the summit of the arch formed by the two rami, even though actual union does not take place for some distance in front of these points (cf. True, 1913<sup>2</sup>, pl. lvii. fig. 2), which probably indicate the potential length of the symphysis



neighbourhood of the coronoid process. The dorsal surfaces of the two rami, in the symphyseal region, are but slightly inclined to one another, so that the symphysis is nearly flat above, as contrasted with *M. bidens*, in which these surfaces have a much greater slope, giving rise to a trough-shaped symphysis.

The mandible of *M. hectori* has a very different shape, being narrow and rounded at the tip, the lateral outlines of the anterior parts of the rami not having the straight character distinctive of *M. mirus*. At from 30 to 140 mm. from the tip the outline is gently concave, and the dentary groove is distinctly curved outwards just behind the posterior end of the symphysis, which is flat above, as in *M. mirus*.

*Vertebral column.*—The vertebral formulae of the two skeletons of *M. mirus* seem to be as follows:—

Liscannor ... C.7; D.10; L.10; Ca.19+. Total, 46+.

Galway ..... C.7; D.10; L.11; Ca.17+. Total, 45+.

The first three cervicals are fused, and one or more vertebrae are wanting at the end of the tail, in both cases. In the Liscannor skeleton one vertebra is certainly missing, and more probably two; which would raise the total to 48. The formula of the Galway specimen is taken from Anderson (1910, p. 117), who gave no further details.

The numbers given above are quite typical for species of *Mesoplodon*, in which the total is 44 to 49, including usually 10 thoracic (9 or 11 occasionally recorded) and 9 to 12 lumbar. It must be remembered, however, in comparing the observations of different authorities, that there is often some uncertainty with regard to the denomination of vertebrae at the junctions of the thoracic, lumbar, or caudal regions.

The number of fused cervical vertebrae is a character of systematic importance in Ziphiidae. In *Hyperoodon* all seven are ankylosed. In *Ziphius* from three to six are fused (Flower, 1878, p. 429); while in *Berardius* and *Mesoplodon* the typical number is three. In *Mesoplodon* there are a few records of specimens with only the first two vertebrae ankylosed; but in several of these cases the animal is known to have been young, and in each instance other skeletons of the same species have three fused cervicals. Thus of the skeletons of *M. grayi* in this condition recorded by Flower (1878, p. 429) one is known to have been young, and the same is true of the *M. layardi* recorded by Oliver (1922, p. 574). *M. bidens* has usually been stated to have three fused cervicals, but the Rosslare individual in the British Museum was young, and two only are fused.

I have used the specimen last mentioned for comparison, and its history may conveniently be given in this place. It is No. 43 of my Report No. 2 on British Stranded Whales (1915, pp. 6, 7, 10), and it has been registered with the numbers 1914.9.28.1. It was stranded alive at Rosslare, Co. Wexford, and as it was

received in the flesh at the Museum it was possible to ascertain its sex (female). The mandibular teeth were concealed beneath the gum during life, and in the prepared jaw they barely project beyond their alveoli, their apices being directed backwards. The total length of the animal was 11 feet 10 inches; and its immaturity is shown by the fact that all the vertebral epiphyses, even in the cervical and caudal regions, are easily detachable. The Liscannor *M. mirus*, on the other hand, has all the epiphyses firmly ankylosed, even at the middle of the body, and is thus fully adult (*cf.* Flower, Proc. Zool. Soc. 1864, p. 386).

The differences between the vertebræ of these two skeletons may be accounted for partly by the difference in age; and the incomplete ossification of some of the neural arches, the ankylosis of two only of the cervical vertebræ, and the delicate character of the processes in the Rosslare skeleton are probably evidences of immaturity. In certain other respects, to which I call attention, the characters of *M. mirus* appear to differ from those of *M. bidens*.

*M. mirus* (Liscannor).—The fused mass of the first three cervicals is of considerable size, its greatest width (across the inferior transverse processes of the atlas) being 199 mm., the width across the similar processes of the axis 163 mm., and across the two articular cavities for the condyles of the skull 118 mm. The vertical height of one of these cavities is 78 mm., and the length of the conjoined centra 58 mm. ventrally. At its anterior end, the neural arch of the atlas has a deep groove for the sub-occipital nerve, a condition which Flower (1872, p. 225; 1878, p. 429) noted as occurring in *Berardius arnucii*\*. The greater part of this mass is formed by the atlas, as the neural arches of the second and third cervicals are thin, although the centrum of the axis is better developed and has two massive inferior transverse processes. The neural spine is stout and pyramidal, with three main faces, and is directed obliquely backwards. It appears to belong almost entirely to the atlas, the axis making but a small contribution to the spine, and C. 3 none at all, the fusion being very complete in this region. Each of the three vertebræ has a pair of inferior transverse processes (parapophyses) in series with those which follow. Those of the atlas are massive, with a diameter of 26 mm. (stouter on the left side) and a length of about 22 mm., and they are directed slightly backwards. The parapophyses of the axis, with a more posterior direction, and situated more ventrally, are rather thinner (diameter 20 mm.) and longer (31 mm.). Those of C. 3 are very different in form, being flattened in the antero-posterior direction, 18 mm. broad at the base and more or less pointed, their length 39 mm. The superior transverse processes (diapophyses) are represented on the atlas by

\* A skeleton of this species (Brit. Mus. 96.11.20.1) has a complete foramen for the nerve.

a vestigial vertical ridge, on the axis by a more prominent ridge, prolonged ventrally into a short point directed towards the parapophysis, and on C. 3 by a flattened but short process, 23 mm. across at its base. Union of the diapophysis and parapophysis does not occur in these or in any of the other cervicals, and there are thus no complete vertebrarterial canals.

In the remaining cervicals, definite neural spines are present. The spine of C. 4 is short and vertical, that of C. 5 directly slightly forwards, its tip nearly touching the spine of the atlas. C. 6 and C. 7 are completely ankylosed by their neural spines, while the upper parts of the neural arches are united on the left side only. The right half of the neural arch of C. 6 is quite free, and it has even failed to unite with the left half. C. 7 appears to form most of the neural spine, which is directed slightly forwards, so as to be not far separated from that of the atlas. It may be noted that ankylosis of two of the two posterior cervicals has previously been recorded by Oliver (1922, p. 570) in a specimen of *M. bowdoini*, in which the neural arches of C. 4 and C. 5 were united, on the right side only.

The parapophyses of C. 4 and C. 5 are long, rod-like (though wider at their bases), and curved backwards, that of C. 4 being 43 mm. long, and that of C. 5 36 mm. Those of C. 6 are much larger, laterally compressed and directed more ventrally than their predecessors, with a greatest diameter of 21 mm. and a length of 36, 30 mm. (R, L). C. 7 has definite indications of parapophyses on the ventral side of the facet for the capitulum of the first rib, which is situated between the diapophysis and parapophysis. On the right side the processes are conical and 15 mm. long, in series with the other similar processes, while on the left side there is merely a low tubercle in a corresponding position. Diapophyses are not well developed in C. 4-6, being small triangular lobes in C. 4 and C. 5 and vestigial in C. 6. The only vertebra in which the diapophyses are really strong is C. 7, in which they are large flattened wings inclined forwards, like the base of the neural arch from which they arise, and are twisted in such a way that the upper edges lie in advance of the lower. They are 23 mm. long and 27 mm. high, and they project outside the corresponding processes of the two vertebræ next in front.

*M. bidens*, juv. (Rosslare).—Vertebral formula, C. 7; D. 9; L. 11; Ca. 18 (+ 1?). Total, 46. It is probable that not more than one vertebra is wanting at the tip of the tail. The neural arches are imperfectly ossified, those of C. 3 and C. 4 being incompletely closed dorsally; C. 5 being just complete but without a neural spine, C. 6 having a short spine, and C. 7 a longer one. The ankylosed atlas and axis have a dorsal, massive portion corresponding with the base of the neural spine in *M. mirus*, but no actual spine is developed. The neural spines are all nearly erect, and there is no approximation of the spines of the two ends of

the neck. The foramen for the suboccipital nerve is completely closed, a condition described by Flower (1878, p. 429) in *M. grayi*; but differing from the open groove of *M. mirus*. The ankylosed atlas and axis measure 128 mm. across the parapophyses of the atlas, and 135 across those of the axis. The width is thus greatest across these processes, not across those of the atlas as in *M. mirus*. The distance across the two articular cavities of the anterior side is 100 mm., while the vertical height of one of the cavities is 61 mm. The antero-posterior length of the fused bodies is 38 mm. ventrally. As in *M. mirus*, the greater part of the mass is formed by the atlas. The parapophyses agree in general with those of the same species, but that of the axis is weaker and is compressed antero-posteriorly. Those of C. 3-5 differ moreover by being high and much compressed antero-posteriorly, the vertical diameter in C. 4 being 20 mm. (L). In C. 5 the processes are somewhat twisted, projecting further ventrally than their predecessors, while in C. 6 they resemble those of *M. mirus*. In C. 7 they are represented by mere vestiges, with a relation to the facet for the rib as in that species. The short diapophysis of the axis is connected with the base of the parapophysis by a thin slip of bone, on each side; and typical, small vertebrarterial canals, 15 mm. in height (R), are thus formed. The posterior end of the same vertebra is provided with a separable epiphysis. The vertebrarterial canal of C. 3 is complete on the left side, and nearly complete on the right. The canal is indicated, but is incomplete externally, in C. 4 and C. 5, while in C. 6 the two processes are so divergent that the canal is not apparent. The diapophyses are thin and triangular in C. 4 to C. 7, the last of which is the strongest, and is directed forwards as in *M. mirus*.

It seems probable that some of the differences between the two specimens do not depend on age. There appear to be real distinctions between the two species in the form and proportions of the diapophyses and parapophyses. *M. mirus* is remarkable for showing no tendency to form closed vertebrarterial canals, while the absence of a complete foramen for the suboccipital nerve is another noteworthy feature.

*Thoracic vertebrae and ribs.*—I have not noticed any differences in principle between the two species in the characters of these vertebrae, which form a series in which the length of the centrum and the size of the neural spine progressively increase, in passing backwards. Thus in *M. mirus* the centrum of D. 1 is 28 mm. long, of D. 2 36 mm., and of D. 3 50 mm. The facet for the capitulum of the second right rib is inconspicuous in D. 1, but the facets are otherwise strongly developed in D. 1-6. Those for the tubercles of the ribs are conspicuous in D. 1-7. Metapophyses commence in D. 3, where they have the form of strong, forwardly-directed hooks, best developed on the right side. D. 1-7 are provided with diapophyses given off from the neural arches, but this series ends abruptly with D. 7; D. 8-10

having parapophyses only\*, on D. 10 resembling the following lumbar processes except by having articulations for ribs, confined, however, to the posterior parts of the processes. In D. 7 distinct vestiges of the parapophyses are present, on the anterior half of the centrum, below the articulations for the tubercles of the ribs; while in D. 6 there is a small conical tubercle in the corresponding position, on each side. The ribs are 10 in number on each side, though the possibility is not excluded that there may have been a pair of vestigial eleventh ribs; and the first seven ribs are provided with capitulum and tubercle. The first rib articulates with the seventh cervical vertebra by its capitulum, and with the transverse process of the first thoracic by its tubercle; the others with a corresponding relation to the subsequent vertebræ. The first and second ribs are specially broad and strong, the first being 100 mm. across at its dorsal end, and 39 mm. at its smallest part, 115 mm. from the ventral end. Measured in a straight line, the first ribs are 385 and 391 mm. long, the second pair 535 and 538 mm., and the fifth pair (the longest) 723 mm. The dorsal end of the tenth rib is not developed on the right side, where it comes to a point, increasing in size ventrally.

The centrum of D. 10 is 102 mm. long, its transverse processes 294 mm. from tip to tip and 65 mm. in diameter at the middle, expanding slightly at the outer ends. The neural spine is 260 mm. high, measured from the neural canal, and its antero-posterior diameter is 75 mm. The neural spine of D. 1 is much smaller, 128 mm. high, 39 mm. in greatest antero-posterior diameter and becoming narrower dorsally, where it ends in a rounded tip. From about D. 5 the neural spines increase rapidly in height and width, becoming truncate and expanded dorsally, a process which is continued in the lumbar series. A ventral carina is beginning to be indicated in D. 8, becoming distinct in D. 9 and 10.

In *M. bidens* (Rossi) D. 1-7 have diapophyses only, except that D. 7 has slight longitudinal ridges on the anterior half of its centrum, apparently vestiges of the parapophyses; while D. 8 and 9 have parapophyses only. The first seven ribs have capitulum and tubercle, and articulate as in *M. mirus*. The eighth and ninth ribs are not "two-headed," and they articulate with the parapophyses of the corresponding vertebræ. Metapophyses are first distinguishable on D. 6, where they are just indicated. Nine pairs of ribs are present, the first two pairs having the same conformation as in *M. mirus*, but being much smaller. Thus the dimensions of the first rib are:—length 255 mm.; diameter, dorsally, 58 mm.; at its smallest part, 70 mm. from the ventral end, 33 mm. The second rib is 359 mm. long.

*Lumbar vertebræ*.—(1) *M. mirus*. The increase in size continues, almost to the end of the series, particularly in the length

\* I hope to have another opportunity of discussing the significance of this remarkably abrupt change, which is specially characteristic of Ziphiidæ and Physeteridæ.

of the centrum and the height and diameter of the neural spines. In a genus remarkable for the great development of the neural spines, *M. mirus* has these structures specially large, their anterior and posterior borders being nearly parallel, the dorsal borders truncate. The greatest size is reached near the end of the lumbar series, the maximum measurements being:—greatest height, 450 mm.; width across transverse processes, 323 mm.; length of centrum, 160 mm.; height of neural spine, from neural canal, 335 mm.; antero-posterior diameter of neural spine, dorsally, 131 mm.; at its middle, 87 mm. The ventral carina, which commenced in the posterior thoracic region, continues through the lumbar series, where it is strongly marked.

(2) *M. bidens*. The lumbar region resembles that of *M. mirus*, but the vertebrae and their processes are conspicuously smaller. The largest vertebra, towards the end of the lumbar region, measures:—greatest height, 291 mm.; length of centrum, 103 mm.; height of neural spine, 192 mm.; antero-posterior diameter of neural spine, dorsally, 75 mm.; at its middle, 55 mm. The ventral carina is well marked throughout the lumbar series.

*Caudal vertebrae*.—The series diminishes in size from front to back, in both species; in *M. mirus*, rapidly after Ca. 5. Instead of the single carina of the lumbar vertebrae, Ca. 1 has two ridges posteriorly, for the articulation of the chevron-bone. The last vertebra with a neural arch, corresponding, as is known in other species, with the commencement of the tail-flukes, is Ca. 11 in *M. mirus*, and Ca. 8 in *M. bidens*. The last distinct zygapophyses are on Ca. 8 and Ca. 6, respectively. In *M. mirus* the only vertebra with a perforated transverse process is Ca. 7, on the right side only. In *M. bidens* the process is perforated, on the left side only, in Ca. 4 and 5, and on both sides in Ca. 6, after which transverse processes cease to be distinguishable. Ca. 4 has a wide emargination on the right transverse process, corresponding with the foramen of the other side. The number of chevron-bones which have been preserved is 9 in *M. mirus*, and 7 in *M. bidens*.

*Sternum* (Pl. IV. fig. 7).—The sternum of *M. mirus* has a considerable resemblance to that of *M. densirostris*, as figured by Andrews (1914, pl. xviii. fig. 1), particularly in the large size of the first segment and in the small size of the median fontanelles. These apertures are, relatively, much larger in the young *M. bidens*; but this particular difference is no doubt due partly to immaturity. Prof. Mangan has sent me a drawing, natural size, of the sternum of the Galway *M. mirus*, indicating, by comparison with the Liscannor specimen, that the characters are variable in the species, or that the male and female are not altogether alike. The more noteworthy differences are as follows:—The second and third segments are relatively shorter in the Galway specimen, the fourth segment is bifurcated posteriorly, and the fontanelles are much larger. The last

difference, at any rate, is probably a function of age, the Galway specimen having been recorded as 14 feet long, and the Liscannor animal as 17 feet. In both specimens the fourth or last segment shows a fontanelle near its middle, indicating that two original segments have fused.

The following table shows the dimensions of the various parts of the sternum in *M. mirus*, those of the Galway specimen having been measured from Prof. Mangan's drawing, which was probably not intended to give the sizes to the nearest millimetre. S<sup>1</sup>-S<sup>4</sup>=segments of the sternum; F<sup>1</sup>-F<sup>4</sup>=fontanelles. The measurements, in millimetres, are taken so as to give the largest diameters of the parts indicated.

	Sternum, total length.	S <sup>1</sup> , length.	S <sup>1</sup> , width.	S <sup>2</sup> , length.	S <sup>2</sup> , width.	S <sup>3</sup> , length.	S <sup>3</sup> , width.	S <sup>4</sup> , length.	S <sup>4</sup> , width.	F <sup>1</sup> , length.	F <sup>2</sup> , length.	F <sup>3</sup> , length.	F <sup>4</sup> , length.
<i>M. mirus</i> , Liscannor ..	633	254	172	144	140	128	136	135	123	10	15	22	12
<i>M. mirus</i> , Galway ..	437	197	141	95	108	76	106	95	80	34	38	19	14

It will be seen from these measurements that, in both specimens, the first segment is definitely longer than wide. In the Liscannor sternum the second segment is as long as wide; but, with this exception, segments 2 and 3 are wider than long. The fourth segment is longer than wide in both specimens, but as it represents two fused segments, it is really composed of two parts, each of which is wider than long.

The predominance of the first segment, and the fact that it is longer than wide, appear to be characteristic features of *Mesoplo-don*, judging by published figures and descriptions. The only exception I have noted is a sternum of *M. bowdoini* recorded by Oliver (1922, p. 571), in which the first segment, although the longest of all, is rather wider than long. In *Berardius*, with five distinct segments, *B. arnuxii* has the first segment slightly wider than long (Flower, 1872, pl. xxvii. fig. 3) and *B. bairdii* has the two measurements equal (True, 1910, pl. xxxii. fig. 2). *Ziphius*, also usually with five segments, has the first segment wider than long or the two measurements subequal (True, 1910, p. 45). *Hyperoodon* has only three segments, of which the first is about as wide as long (Vrolik, 1848, pl. viii. fig. 17).

The sternum of *M. mirus* resembles that of other species of the genus in bearing articulations for five pairs of ribs, the first in the anterior half of the first segment, the next three at the junctions of the four segments, and the fifth on the last segment, opposite the median fontanelle.

*Scapula*.—(1) *M. mirus*. The scapulæ are both imperfect, especially along their dorsal border, so that the height cannot be given with accuracy. They are considerably longer than high, the length being approximately 380–396 mm., and the height at the middle 260 mm. The acromion curves slightly upwards, its lower border being nearly parallel to the upper border of the coracoid process. The coracoid process is smaller than the acromion, and it expands regularly from its base to a region not far from the tip. Length of acromion, 130 mm.; width (L), 51 mm., the right rather narrower. Length of coracoid process, 104 mm.; width at base, 35 mm.; diameter, oblique, of widened distal end, 58 mm.

(2) *M. bidens*. Scapula longer than high, the acromion straight and short, its lower border slightly diverging from the upper border of the coracoid process, which is not fully ossified. Length of scapula, 244 mm.; height at middle, 157 mm.; length of acromion, 61 mm.; width at base, 33 mm.; length of coracoid process, 50 mm.; width at middle, 19 mm.

*Flippers*.—One of the flippers of the Liscannor *L. mirus* is wanting, and the other is too incomplete to describe. The humerus is 139 mm. in greatest length, and 64 mm. in diameter at its lower end.

MESOPLODON DENSIROSTRIS (de Blainv.).\* (Plates I–IV. figs. 1, 3, 5, 8, 10; text-fig. 2, p. 551, f.)

*Delphinus densirostris* de Blainville, 1817, *Nouv. Dict. Hist. Nat.* 2<sup>e</sup> Éd. ix. p. 178 (A).

*Ziphius sechellensis* Gray, 1846, *Zool.* 'Erebus' and 'Terror' †, p. 28, pl. vi. figs. 1, 2 (skull and lower jaw) (B).

*Dioplodon densirostris* Gervais, 1850, *Ann. Sci. Nat.* (3) xiv. p. 16; 1852, *Zool. et Pal. Franç.*, vol. ii. *Expl. of pl. xl.* and *Atlas*, pl. xl. figs. 3–6 (skull, lower jaw) ‡; 1859, *Ibid.* 2<sup>e</sup> Éd. p. 289, pl. xl. figs. 3–6 (B).

*Mesiodiodon densirostre* Duvernoy, 1851, *Ann. Sci. Nat.* (3) xv. p. 58, pl. ii. figs. 4–4" (skull and lower jaw) (B).

*Dioplodon sechellensis* Gray, 1866, *Cat. Seals and Whales Brit. Mus.* p. 355 (B); 1871, *Ibid.* *Suppl.* p. 102, fig. of skeleton, p. 103 (C); 1870, *Ann. Mag. Nat. Hist.* (4) vi. p. 343, fig. of skeleton (C); 1868, *Syn. Whales and Dolph. Brit. Mus.* p. 10, pl. vi. figs. 1, 2 (*Ziphius sechellensis* on Plate, which is identical with Gray, 1846, *supra*) (B).

\* The letters in brackets correspond with the list on p. 576, and indicate the specimens specially referred to.

† The copy of this work in the British Museum (Natural History) contains a good photograph (unpublished) of a lower jaw, the right tooth in place and the left lying on the stand on which the jaw is mounted. The teeth are of the male type, and the photograph may be the one referred to by Gray (1870, p. 344) as having been sent to him by Mr. Krefft (specimen C).

‡ I have been unable to consult the plates of the First Edition of Gervais' work.



- Dioplonodon sechellensis* Krefft, 1870, Proc. Zool. Soc. p. 426 (mostly reproduced by Gray, 1871) (C).  
*Dioplonodon densirostris* Scott, 1873, p. 118 (C).  
*Mesoplonodon densirostris* Flower, 1878, Trans. Zool. Soc. x. pp. 416-418 (B, C, D); Flower & Garson, 1884, Cat. Ost. R. Coll. Surgeons, Pt. ii. p. 561 (D).  
*Dioplonodon densirostris* and *D. sechellensis* Van Beneden & Gervais, 1868-1879, Ostéogr. Cétacés, p. 406, pl. xxv. figs. 1-1 c (rostrum) (A), figs. 2-2 d, 3-3 a (skull and lower jaw) (B); pl. xxii. fig. 9 (skeleton) (C).  
*Ziphius densirostris* Owen, 1870-1889, p. 34, text-fig. (skull and lower jaw) (B).  
*Mesoplonodon bidens* (pars) G. M. Allen, 1906, p. 357, text-fig. 3, p. 363 (tooth), text-fig. 4, p. 364 (sternum) (E).  
*Mesoplonodon densirostris*? True, 1910, U.S. Nat. Mus., Bull. 73, pp. 2-4, 9, pls. i., iv., vii., x. figs. 2 (skull), pls. xxxiv-xxxvii. figs. 1 (tympanic and periotic) (E).  
*Mesoplonodon densirostris* Andrews, 1914, Proc. Ac. Nat. Sci. Philadelphia, p. 437, pls. xvi. -xviii. (external appearance, skull, lower jaw, sternum and vertebræ) (F).

The previous records of the species appear to be as follows:—

- A. Part of a rostrum, 9 inches long, of unknown origin, in the Paris Museum (type of the species).
- B. Skull, also in the Paris Museum, sent from the Seychelles by M. Leduc in 1839. Gray gave it the name of *Ziphius sechellensis*, and later followed Gervais in placing it in *Dioplonodon*.
- C. Skeleton, nearly complete, in the Sydney Museum, from Lord Howe Island.
- D. Rostrum (No. 2908), from the shore near Algoa Bay, South Africa, in the Museum of the Royal College of Surgeons, London. Presented by C. Westendorp, 1872.
- E. Skeleton, in the Museum of the Boston Society of Natural History (U.S.A.), of a specimen described as a young female, 12 feet 2 inches in length, from Annisquam, Massachusetts Coast, August 1898.
- F. Skeleton, in the Academy of Natural Sciences, Philadelphia, of a fully adult animal, 14 feet 5 inches long, obtained June 18, 1913, at Corson's Inlet, New Jersey, U.S.A.

To these has now to be added the following specimen, of which I give a description below.

- G. Skull, nearly complete, with part of the lower jaw, wanting the teeth, of a specimen stranded at Porto Santo, Madeira, in 1917.

It will be seen from the above list that this species has a wide distribution; being known to occur off the E. coast of Australia (C), and South Africa (D) in Southern waters, at the Seychelles

(B), in the Indian Ocean\*, and in the Atlantic (E, F, G). Like the specimens of *M. mirus* noticed above, the Porto Santo specimen extends the range of a species previously known as a Western Atlantic species to the Eastern side. I am indebted to Mr. R. H. Burne for having lent me the rostrum (D) belonging to the Royal College of Surgeons.

This remarkable species, distinguished from all others by the characters of its lower jaw and rostrum, was named from an imperfect rostrum (A), about 9 inches (230 mm. long), of unknown locality, in the Paris Museum. Van Beneden and Gervais state (p. 406) that de Blainville mistook this specimen for a lower jaw; but, in justice to the original describer, it should be pointed out that his actual words are "Ce fragment qui présente la pointe de la mâchoire supérieure." Gray unnecessarily proposed a new trivial name, *sechellensis*, for specimen B, while admitting *densirostris* into his synonymy. B and C are the only ones in which large teeth, presumably of the male type†, have been observed. In 1910 True published an account, mainly of a female skull (E), which he referred doubtfully to this species, quoting observations by Glover M. Allen (1906) on its external appearance and skeleton. The next record (F), by R. C. Andrews, is particularly interesting in including a figure of the animal in the flesh, with a description of the skull and other parts of the skeleton. The teeth figured by him appear to be of the female type. He expresses the opinion, with which I concur, that True's specimen (E) certainly belongs to this species. It will be seen that the recorded occurrences of *M. densirostris* have been very sporadic (Seychelles, S. Africa, Lord Howe Island, Western North Atlantic).

During a visit which I made to Madeira in the spring of 1923, Senhor A. C. de Noronha showed me a skull in his possession, at the Museum of the Seminario, Funchal. It obviously belonged to *M. densirostris*, which, although recorded from the Western North Atlantic by True and Andrews, had not been found previously on the Eastern side of that ocean. Senhor de Noronha had the great kindness to make arrangements for the transference of the skull to the British Museum, where it is now preserved; and he gave me the following account of its history:—The animal was stranded on the Island of Porto Santo, Madeira group, in 1917, having been trapped by a sand-bank extending along the coast of the "grande plage," and thus having been unable to escape when the tide fell. The head was separated from the body by his father, the late Senhor A. N. de Noronha, and after having been cleaned by being buried in the sand, it was sent to Madeira in the following year. No notes were kept with regard to its size, sex or external characters. The large size of the alveoli of the mandibular teeth point, however, to the animal

\* Weber (1923, p. 3) mentions a record from the Malay Archipelago, but he is not satisfied that it can be accepted.

† This conclusion is stated by Owen (1870-1880, p. 34).

having been a male. The measurements and special description which follow refer to the Porto Santo specimen unless the contrary is stated.

*Skull*\*, *dorsal view* (Pl. I. fig. 1).—The rostrum is highly ossified throughout, and to such an extent that the premaxillæ in particular have lost their distinctness of outline. The mesorostral rises definitely above the level of the premaxillæ at its posterior end, which lies nearly in the transverse plane including the anterior ends of the prenasal expansions of the premaxillæ. It becomes lower in passing forwards, but it remains slightly above the premaxillæ throughout the posterior half of the rostrum. It is so intimately ankylosed with the adjacent bones that the point at which it terminates in front cannot be ascertained.

Between the prenasal expansions of the premaxillæ the thickened edge of the mesethmoid is deeply depressed, but the bone rises to a higher level at the front of the nares. It here forms a thin internasal septum, in which is a deep and narrow sinus, limited in front by a portion which rises abruptly from the depressed thickened edge, and behind by another portion, passing above the level of the premaxillæ, and ending in a free edge thickened as a short triangle having its base in contact with the nasals.

The antorbital notches are distinct, the interval between their deepest portions being 185 mm., which may be regarded as the width of the rostrum at its base. The characters of the antorbital region have been described above (p. 552). Maxillary tuberosities are barely indicated, and the maxillary tubercles are indistinct. Behind the tubercles the dorsal surface of the rostral portion of the maxillæ becomes concave, and this conformation is accentuated further back. The concavity increases until it finally becomes a complete tube at the posterior end, where it is continuous with the maxillary foramen. It is possible that this tubular portion has been formed by a concrescence of adjacent parts of the maxilla and premaxilla. True (1910, p. 9) has already commented on the deeply grooved character of the maxillæ in this region. He obviously regarded the point at which the tube becomes an open groove as the maxillary foramen, which he accordingly described as being in front of the premaxillary foramen. If the above suggestion that concrescence has occurred is correct, the maxillary foramen is situated behind its apparent opening. On the left side the posterior end of the open groove is sharply pointed, and exactly the same feature is seen in the College of Surgeons rostrum (D) and in True's figure (pl. i. fig. 2). On the right side the corresponding part is rounded, but the rostrum D is broken at this point, the fracture passing along the right maxillary foramen. The interval between the posterior ends of the grooves is 65 mm. in the Porto Santo skull.

\* For measurements see table on p. 560.

The premaxillary foramina are small, and are 31 mm. apart. The exposed surface of the mesorostral diminishes gradually in width in passing forwards, and, so far as can be seen in the co-ossified mass, the interval between the premaxillæ is not more than 3-4 mm. at a point 220 mm. from the tip of the rostrum \*. The premaxillæ then divaricate gradually to the tip, which is bifid; and just behind the tip their dorsal edges are 13 mm. apart.

At the inner notches, which are about 40 mm. in advance of the antorbital notches, the rostrum is 95 mm. wide. The maxillary flanges, which commence at the maxillary tubercles, are small, with a maximum diameter of 25 mm., and they disappear at about 80 mm. in front of the inner notches. Their general line is continued, shortly in advance of this point, as the upper or median limit of a very shallow groove, the floor of which is formed by the ivory-like bone which constitutes most of the rostrum. About 120 mm. in front of the inner notch the edge commences to rise again (Pl. III. fig. 5), passing down the side to the ventro-lateral surface, where it becomes strongly marked, adding appreciably to the width of the rostrum. The part of the rostrum which lies between 300 and 400 mm. from its tip is distinctly compressed laterally, and its greatest width is only 48 mm. at a distance of 330 mm. from the tip. In front of this part the rostrum widens to 61 mm., largely owing to the strong projection of the above-described ridges, which are now ventro-lateral. In this region the rostrum is narrow dorsally and broad ventrally, so that its transverse section would be sub-triangular. The dorsal surfaces of the premaxillæ have here assumed a lateral and sub-vertical position.

Behind the rostrum the premaxillæ form the usual prenarial expansions, their greatest width being 50 mm. (R) and 41 mm. (L). Their least width, opposite the anterior nares, is 33 mm. (R) and 25 mm. (L). They expand as they rise behind the nares, and at the level of the edge of the mesethmoid in contact with the nasals they have reached a width of 54 mm. (R) and 40 mm. (L). The proximal edges are but slightly revolute, but the end of the left premaxilla is broken off, and its shape cannot be stated. The prenarial expansions are so slightly convex that they are practically flat. They are traversed by a shallow groove, which starts from the premaxillary foramen, immediately bifurcating, the outer branch passing in a curve backwards along the outer border of the expansion, the inner branch passing obliquely across the expansion to the hind portion of its straight inner edge.

As compared with *M. mirus* the orbital plates of the maxillæ slope inwards and upwards to the vertex, without assuming so completely vertical a position as in that species. The frontal is uncovered, at the middle of the orbit, for a width of only 3-4 mm.

\* As in fig. 2, the rostrum of fig. 1 is marked by paper slips 60 mm. apart.

The edge of the maxilla continues backwards behind the orbit, the uniformity of the curve being interrupted above the anterior part of the temporal fossa. At the vertex the maxillæ form rather short lobes behind the raised premaxillary crests, and their edges are thin, instead of being thickened as in *M. nirus*. The principal measurements of these parts of the maxillæ are:—tip of maxillary tubercle to hind end of maxilla, 242 mm.; width of maxilla at middle of orbit, 105 mm.; edge of maxilla at middle of orbit to edge of dorsal part at vertex, 208 mm.; length of dorsal part of maxilla behind premaxillary crest, 40 mm.

The nasals are much smaller than in *M. nirus*, both considerably below the level of the premaxilla, and the outer lobe of the right bone not reaching the summit of the premaxillary crest. The outer lobe of the left nasal is wanting, with part of the premaxillary crest and of the frontal on the same side. The nasals have a very small horizontal component, and their suture, 43 mm. long, is almost entirely vertical, their anterior surfaces forming the hind wall of the commencement of the nasal passages.

The malars are visible, in dorsal view, at the posterior end of the antorbital notch, the longitudinal diameter of the part here exposed being 8 mm. (R) and 5 mm. (L).

*Lateral view* (Pl. III, fig. 5).—This view shows one of the most characteristic features of the species, the form and the proportions of the rostrum, which is deeper than wide along its whole length, except close to its two ends. This fact is brought out by the following measurements, taken at regular intervals of 60 mm. from the tip, as marked on the skull. The height is measured in the middle line, while the next column gives the greatest width at any part of the transverse section.

	Distance from tip of rostrum.	Height.	Width.
A . . . . .	60	28	28
B . . . . .	120	44	38
C . . . . .	180	57	52
D . . . . .	240	70	61
E . . . . .	300	87	51
F . . . . .	360	94	55
G . . . . .	420	103	72
H . . . . .	480	116	98 *

These measurements show that the rostrum diminishes in height from its base to its tip, but that in the region E-F it is more compressed laterally than in front and behind. H lies about 25 mm. in front of the premaxillary foramen, G behind the anterior end of the pterygoid, and F behind that of the palatine. The dorsal outline is slightly concave from B to E, gently convex elsewhere. The ventral outline is slightly concave behind E,

\* This is the width at a point equidistant from the dorsal and ventral surfaces. Measured so as to include the maxillary tubercles, the width is 168 mm.

then convex, most so between D and E, and again concave, mostly below B. The dental groove is very shallow, its floor being formed by dense, ivory-like bone like that of most of the rostrum; and in this specimen, which is obviously adult, the basirostral groove which Flower (1878, p. 418) describes as deep, does not exist except as a vestige. The groove is bordered dorsally by a sharp ridge, which is obsolete at F, re-appearing between F and E. The ridge commences at the maxillary tubercle, where it constitutes the edge of the small lateral flange of the maxilla. After dying away at F, it continues its course down the sides of the rostrum to near its ventral side, between C and D. At D, where it reaches its greatest development, it is a strongly-projecting ridge, which projects outwards and downwards, and the presence of these ridges, on the two sides, materially adds to the width of the rostrum in this region. At C the ridge is diminishing in height, and it has almost disappeared at B, while at A it is just indicated as a slight rounded longitudinal swelling.

The rostrum in the College of Surgeons agrees closely with the Porto Santo rostrum in the extent of its ossification, particularly of the mesorostral bone. Its actual measurements are rather smaller, but its size has probably been appreciably diminished by being waterworn. Making full allowance for this, it seems to have been more slender than the Porto Santo rostrum, but did not differ from it much in length. It may be estimated that a length of about 70 mm. of the tip of the rostrum has been lost by wear, the total length of the fragment being 500 mm. It has been broken off at the level of the maxillary foramen on the right side, and somewhat behind this point on the left. The distance from the tip to the anterior vertical edge of the internasal septum is 468 mm., which, on the above estimate, would be 538 mm. if the tip were complete. The corresponding measurement of the Porto Santo skull is 563 mm.

In the antorbital region the lachrymal is barely visible in a completely lateral view, but if viewed slightly from the ventral side its characteristic thin edge can be seen, considerably overhung by the frontal. Posteriorly, where its edge is slightly thickened, it is even more overhung, and is directed more ventrally than laterally. The temporal fossa is not nearly so deep posteriorly as in *M. mirus*, its greatest vertical diameter being 62 mm., and its length, measured obliquely to its anterior point, being 95 mm. The oval groove on the outer side of the squamosal is much shallower than in *M. mirus*. The pterygoids are injured ventrally. Their posterior notch is narrow, more so ventrally than further dorsally, and their external concavity is not subdivided. The palatines are 56 mm. high below the antorbital notch, diminishing suddenly at the anterior end of the pterygoid, and there 22 mm. high. A considerable strip of the palatine, 11-15 mm. wide, is visible (in ventral view) on the inner side of the pterygoid, reaching back for about 165 mm. from the tip of the palatine, and ascending up the inner side of the pterygoid.

*Ventral view* (Pl. II. fig. 3).—A few minute foramina for vessels or nerves are visible in the dentary groove, in a series extending from the tip of the rostrum to about half-way between C and D. In consequence of the co-ossification of the bones, the limits of the vomer are uncertain. The palatal surface has a longitudinal, median ridge in front, from about A to D, with foramina much as described in *M. mirus*. The next part of the ventral surface then becomes uniformly convex, to just beyond E, where the median ridge re-forms, and becomes prominent between the tips of the palatines and of the pterygoids, the tips of which are 34 mm. behind those of the palatines.

*Mandible* (Pl. IV. figs. 8, 10).—Although the mandible is incomplete, it is fortunate that the anterior part of the left ramus overlaps the posterior end of the right ramus, so that every part except the teeth is represented. The portions preserved are (a) a piece about 455 mm. long, including the right ramus, complete to just behind the dorsal prominence bearing the tooth, and the anterior part of the left ramus as far as 255 mm. from the tip, or just in front of the tooth-region; (b) the posterior part of the left ramus, about 370 mm. long, complete from the posterior border of the tooth-region to the condyle. It seems clear that the left ramus had been broken in order to extract the tooth (wanting on both sides), and the right side is marked by cuts of some sharp instrument. The length of the mandible, when complete, appears to have been 660 mm., and its principal measurements are as follows:—

A.	Height of ramus (outer border), 90 mm. from tip	45
B.	" " at posterior border of symphysis	72
C.	" " at anterior end of alveolus...	137
D.	" " at posterior " "	167
E.	" " 16 mm. behind raised dorsal part	133
F.	" " at posterior end	128
G.	" " condyle	45
H.	Tip to anterior border of alveolus (straight)	262
I.	Length of alveolus	72
J.	" post-alveolar raised part	105-120
K.	" posterior lower part (upper border)	216
L.	" symphysis	197
M.	Width of jaw, 90 mm. from tip	53
N.	" " at posterior end of symphysis	104

The jaw is narrow at its anterior end, the ventral outline being here nearly straight. The ventral border then turns up, at an angle of 30°, from just in front of B, and from there to E is distinctly concave, after which it becomes nearly straight to the posterior end. The dorsal outline is at first straight, then sweeping up in a bold concavity, the middle of which is in front of the posterior end of the symphysis. The alveolus commences at the end of this concavity, and its opening continues to ascend, so that it faces to some extent anteriorly as well as dorsally.

Behind the alveolus the outline of this part of the jaw, which is much elevated, is horizontal, with a thick, rounded edge, overhanging outwards at its posterior end. The outline then falls steeply, so that the posterior part of the jaw is considerably lower than the region immediately behind the tooth. There is no distinct indication of a coronoid process, and the dorsal outline finally ascends to a prominent point above the condyle, which is at about the middle of the posterior, vertical border. The point just indicated passes, on the outer side, into a ridge, which slopes downwards and anteriorly. The maximum longitudinal swelling of the outer surface of the ramus starts at the condyle and passes ventrally, a strong concavity of this surface being found below the hind part of the raised post-alveolar part of the jaw.

The symphysis is measured to the summit of the arch formed by the two rami, but the bones do not actually meet in the posterior part of this region, which is slightly trough-shaped dorsally, the two sides sloping down to the middle line. The dentary groove commences at the front of the jaw, and is distinct as far as the alveolus, but not beyond it. The alveolus is 26 mm. wide, its inner edge nearly straight, its outer edge concave inwards, and it is 130 mm. deep. The missing teeth were thus of large size, and appear to indicate an animal of the male sex.

*M. densirostris* appears to occupy an isolated position in the genus, and there seems to be no other species to which it has near affinities.

In view of the extreme rarity of this species it is worth while to bring together the few observations which have been recorded with regard to its external appearance, size, and skeletal characters. The specimens are distinguished by the letters assigned to them on p. 576.

*External appearance.*—The only published figure seems to be that of F (Andrews, 1914, pl. xvi.). The most striking feature is the extraordinary form of the lower jaw, the dorsal outline of which slopes upwards from the tip, in correspondence with the shape of the anterior part of the mandible. The curve culminates in a large and prominent tubercle, overlapping the rostrum and corresponding with the position of the tooth, which is not visible in the side view represented. The dorsal outline forms a sinus behind the tubercle, and the angle of the jaw, which was presumably further back, is not visible. The eye is situated at a low level, and is in line with the dorsal border of the anterior, narrow part of the lower jaw. If my interpretation of the figure is correct, the structure near the ventral surface, which looks like the mouth, is the left throat-groove. I venture to think that this figure does not give a really satisfactory idea of the shape of the head and mouth.

*Colour.*—Specimen F (Andrews, 1914, p. 438). Mostly uniform blackish, smooth and shining. Livid pale areas, sometimes bluish, occurred about the head and jaws, and ventrally. All the fins were black. Allen (1906, p. 361) records certain



features of E, including a few external measurements, as noted by Prof. Hyatt. Although there was no information about the colour, photographs seemed to show that the ventral portion was of a lighter tint than the back, and a few oval whitish spots were seen on the side, a trifle behind the middle of the body.

*Total length.*—Kreffit (1870), quoted by Gray (1871, p. 102), stated that the skeleton of C was 14 feet 8 inches long "without cartilage." The total length of the animal was presumably somewhat greater. True (1910, p. 10) gives the length of E as 12 feet 2 inches, on the authority of Prof. Hyatt. With the exception of two or three of the cervicals, all the vertebrae had free epiphyses, and the specimen was accordingly young. Andrews (1914, p. 438) records a length of 14 feet 5 inches for F, the animal being fully adult, as shown by the ankylosis of the vertebral epiphyses. The maximum length indicated by these figures is in the neighbourhood of 15 feet.

*Sex.*—E was recorded as a young female (True, 1910, p. 3), and the teeth barely projected above their alveoli. From True's figure (Pl. I. fig. 2) it is evident that the mesorostral was far less ossified than in the Porto Santo and other specimens. The sex is not recorded in the remaining specimens, but from the appearance of the teeth shown by Andrews in pl. xviii. fig. 7, in the fully adult specimen F, it is probable that this also was a female. Judging by the characters of the rostrum and teeth (or their alveoli), it appears to me that B, C, and G were males, and that the rostrum D probably belonged to an animal of the same sex.

*Skull, total length.*—True (p. 8) gives this in E as 622 mm., adding an estimated length of 31 mm. for breakage, and thus estimating the total as 653 mm. Krefft, quoted by Gray, gives 2 feet 5½ inches (=750 mm.) for C. The Porto Santo skull (G) is actually 740 mm. long, but as the occipital region is deficient behind, 25 mm. may be added, making a total of 765 mm. The specimen is thus among the largest known, and may be supposed to have been fully adult, a conclusion supported by the great amount of ossification of the mesorostral bone.

*Mandibular teeth.*—In C (Kreffit), 6 inches (152 mm.) long, 3¾ inches (85 mm.) antero-posterior width, 1¾ inches (44 mm.) transverse width. The alveolus of the Porto Santo specimen (G) is 130 mm. deep, 72 mm. in antero-posterior diameter, and 26 mm. in transverse diameter. The tooth of the female specimen (E) is figured by Allen (1906, p. 363) and was 55 mm. long and 30 mm. broad at the base, these measurements being notably smaller than those of the two preceding specimens.

*Vertebral formula.*—Andrews (p. 439) gives for F, C. 7, D. 10, L. 11, Ca. 16 (+2 ?), total 46 (?); C. 1-3 being fused. For E, True gives C. 7, D. 9, L.+Ca. 29, total 45; C. 1-3 firmly ankylosed, and C. 4 fused to C. 3 by the neural spine and by the tip of the diapophysis, on the left side, with C. 3. Gray's account (1871, p. 102), based on Krefft's description of C, contains several conflicting statements; but, from an examination of the figure,

I think the vertebral formula was probably C. 7, D. 10, L. + Ca. 28, total 45. C. 1-3 were fused; "the next one is more or less free." The numbers thus recorded show a close agreement. Some of the separate vertebræ are figured by Andrews (1914, pl. xviii. figs. 3-6).

*Sternum*.—Allen (1906, text-fig. 4, p. 364) figures the sternum of E, a young specimen, the anterior segment being imperfectly developed. Andrews (1914, pl. xviii. fig. 1) shows an older sternum, in which the first segment is much more developed, its anterior end being strongly emarginate in front, and the lateral processes in the region of the articulations of the ribs being prominent. In both these cases four segments are present, and the same number is recorded by Kreffit, who gives the total length as 20 inches (508 mm.).

*Scapulae*.—Figured by Andrews (pl. xviii. fig. 2) in F.

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## EXPLANATION OF THE PLATES.

## PLATE I.

Skulls of *Mesoplodon*, in dorsal view. The rostrum is marked, in each case, by a series of paper slips 60 mm. apart. For sizes see table on p. 560.

Fig. 1. *M. densirostris*, presumably male, Porto Santo. The posterior part of the occipital, including the condyles, is wanting, and the bones of the left side of the vertex have lost their dorsal ends. (Brit. Mus.)

Fig. 2. *M. mirus*, male, Liscannor, Co. Clare. (Brit. Mus.)

## PLATE II.

The same skulls, ventral view.

Fig. 3. *M. densirostris*. Zygomatic portions of malaræ and condylar region of occipital wanting. Pterygoids incomplete ventrally.

Fig. 4. *M. mirus*.

## PLATE III.

The same skulls, side view.

Fig. 5. *M. densirostris*.

Fig. 6. *M. mirus*. The mandibular tooth has lost its terminal portion.

## PLATE IV.

Lower jaws and sternum of the same specimens.

Fig. 7. *M. mirus*. Sternum, ventral view (measurements on p. 674).

Fig. 8. *M. densirostris*. Anterior part of the lower jaw, from above. The large alveolus is present on the right side.

Fig. 9. *M. mirus*. Anterior part of the lower jaw, from above. The terminal portions of the teeth were sawn off by the finders of the stranded specimen.

Fig. 10. *M. densirostris*. Lower jaw, seen from the right side. The incomplete left ramus is approximately in its correct position.

## NOTE.—

The respective Plates should be looked at upside down in order to see figs. 1 and 3 to the best advantage. Pl. III. should be studied with its left margin uppermost.



2.



5.



3.



4.

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26. On the Cephalopoda obtained in South African Waters  
by Dr. J. D. F. Gilchrist in 1920-21. By GUY C.  
ROBSON, M.A., F.Z.S.\*

[Received March 4, 1924: read April 15, 1924.]

(Plates I., II. †; text-figures 1-51.)

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I. INTRODUCTION.

During the Marine Biological Survey of South African waters undertaken by Dr. J. D. F. Gilchrist in 1920 and 1921 for the Union Government, a large number of Cephalopoda were obtained in two main areas - one off Cape Town, the other off the Natal coast. This collection was forwarded by Dr. Gilchrist to the British Museum (Natural History) for identification, and two preliminary reports have already been published (Robson, 1924 *a* and *b*).

The present report deals exclusively with the collection, but the data already published are not included in it.

Our knowledge of the Cephalopoda of South Africa is singularly deficient, as no large catches of these animals have been made in this area. A few of the early zoological expeditions, such as those of the 'Astrolabe' and 'Bonite,' took a few specimens off the Cape and Agulhas Bank. In 1848 Krauss, in his 'Südafrikanische Mollusken,' enumerated only nine species (which included four of *Sepia*). The later visits of the 'Novara' and 'Gazelle' were unproductive, while the 'Challenger' obtained only a few species. In 1886 Hoyle drew up a list of South African littoral species, twenty-four in number, and his Atlantic list of pelagic forms included some obtained in South African waters. He delimited a South African "region" (1886, p. 217), without commenting on what is well known, viz. the difference between the faunas of the East and West coasts of South Africa.

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† For explanation of the Plates, see p. 686.



The 'Valdivia' in 1898 obtained a certain number of species off the Cape and Agulhas Bank. But the material obtained in the Guinea Stream and Indian Ocean by that cruise affords a valuable complement to our knowledge of this fauna. The affinities of many of the species concerned were made clearer by Pfeffer's monograph (1912) on the *Cegopsida* of the Plankton Expedition, though the latter did not actually visit South Africa. Among the smaller contributions to our knowledge we must mention those of Thiele (1921), Hoyle (1912), and E. A. Smith (1917).

The collection made by Dr. Gilchrist consists of one hundred and twenty-four specimens (exclusive of unrecognizable fragments), which represent thirty-three species. Of these, ten are new to zoology, one being a new generic form: while there are two new varieties and five forms which are of obscure taxonomic status and therefore unsuitable for final classification. Pelagic and littoral forms are both represented, and three species and two other forms of deep-sea Polypoda were obtained, which enlarge our knowledge of these interesting forms.

## II. LIST OF SPECIES OBTAINED

### Cephalopoda Dibranchia.

#### Sub-order 1. Decapoda.

##### Tribe 1. *Cegopsida*.

##### ONYCHOTEUTHIDÆ.

*Moroteuthis* A.

*Lycoteuthis* sp.

##### ENOPLOTEUTHIDÆ.

*Abralia gilchristi* Robson.

*Octopodoteuthopsis* sp.

##### HISTIOTEUTHIDÆ.

*Histioteuthis bonelliana* (Fér.)

##### OMMATOSTREPHIDÆ.

*Todaropsis eblancæ* (Ball).

##### CHIROTEUTHIDÆ.

*Mastigoteuthis* sp.

##### CRANCHIIDÆ.

*Pyrgopsis pacifica* (Issel).

*Galiteuthis armata* Joubin.

*Liocranchia reinhardti* Steenstrup.

" *intermedia* Robson.

*Cranchia scabra* Leach.

*Anomalocranchia impennis* Robson.

Tribe 2. *Myopsida*.

## SEPIOLIDÆ.

- Heteroteuthis hawaiiensis* Berry, var. *dagamensis* Robson.  
*Rossia enigmatica* Robson.

## SEPIIDÆ.

- Acanthosepion vermiculatum* (Quoy & Gaimard).  
*Rhombosepion capense* (d'Orb.).  
 „ *acuminatum* (E. A. Smith).  
 „ *hieronis* Robson.  
*Doratosepion confusum* (E. A. Smith).  
*Sepiella cyanea* Robson.

## LOLIGINIDÆ.

- Loligo* A.  
 „ B.  
 „ *indica* Pfr.

Sub-order 2. *Octopoda*.Tribe 3. *Cirrata*.

## CIRROTEUTHIDÆ.

- Cirroteuthis gilchristi* Robson.  
 „ A.  
 „ B.

Tribe 4. *Incirrata*.

## BOLITAENIDÆ.

- Eledonella massyæ* Robson.

## POLYPODIDÆ.

- Velolona tugata* Chun, var. *capensis* Robson.  
*Polypus rugosus* (Bosc).  
*Bathypolypus grimpei* Robson.  
 „ (?) *valdiviæ* (Chun).  
*Benthoctopus berryi* Robson.

## III. THE SOUTH AFRICAN MARINE FAUNA.

a. *Evidence from the present collection.*

Of the thirty-three species represented, seventeen were obtained off Cape Town, fifteen from the Natal coast, and one was taken in both areas. This distribution gives an exaggerated idea of the difference between the faunas of the two areas, as *Histioteuthis bonelliiana* is recorded from the Indian Ocean (Thiele, 1921, p. 452) and *Galiteuthis armata* (with a little less certainty) from the Pacific (Sasaki, 1920, p. 200). Of the Natal forms, *Pyrropsis pacifica*, *Liocranchia reinhardti*, and *Cranchia scabra* are

cosmopolitan forms known from the Atlantic. The known distribution and affinities of the species from the two areas may be summarized as follows :—

CAPE TOWN (17 species).

1. Species recorded elsewhere—in Atlantic—1.  
     ,, Atlantic-Indian Ocean—1.  
     ,, Atlanto-Pacific—1.
2. Species only known from the Cape area :  
     With nearest related species in Atlantic—6.  
     "     "     "     "     Indo-Pacific—3.  
     "     "     "     "     Southern Ocean—1.  
     "     "     "     "     Atlantic-Indian Oc.—2.  
     "     "     "     "     ?     —2\*.

NATAL (15 species).

1. Species recorded elsewhere—in Indian Ocean—2.  
     Cosmopolitan—3.
2. Species only known from Natal area :  
     With nearest related species in Atlantic—3.  
     "     "     "     "     Indian Ocean—4.  
     "     "     "     "     ?     —3.

To these we should add *Heteroteuthis hawaiiensis* var. *dagamensis*, which, being found in both areas and being otherwise known from the Hawaiian Is., gives the Cape area an additional Pacific representative and the Natal area an Atlanto-Pacific species.

From this analysis we see that the adjacent Cape and Natal areas are tolerably distinct, as far as the known distribution and affinities of their species are concerned. Of the seventeen Cape species, seven are Atlantic in their distribution or relationship, four are Indo-Pacific, while four are common to both areas (Atlantic and Indo-Pacific). On the other hand, of the fifteen Natal species, six are derived from the Indian Ocean or Indo-Pacific, three are Atlantic, while four (the three cosmopolitan species and *Heteroteuthis hawaiiensis*) are common to both areas.

b. Evidence from other groups.

The difference between these two areas, based as it is in this report upon some thirty-three species, is not of course put forward as characteristic of the whole Cephalopod fauna, especially as the affinities of several of these forms are only provisionally suggested. Nevertheless, the result obtained by the above comparison agrees with the general conception of a distinction

\* I have included *Bathypolypus caldivia* among these. Although it is nearly related to *B. grimpoi* (Natal) I am of the opinion that both these forms are of Atlantic origin.

between the marine faunas of South-West and South-East Africa, due to the marked hydrographical differences between those areas. The sharp contrast between the upwelling Benguela current on the West and the south-going warm Mozambique-Agulhas current on the East has been already described by Gilchrist (1923).

These faunistic differences were pointed out for the Prosobranch and Lamellibranch Mollusca by v. Martens (1874, p. 119) and Gibbons (1877, p. 233), and v. Martens later on delimited three distributional areas—a South-Western area terminating at Cape Point, a Southern area between the latter and Algoa Bay, and a Natal area (1903, p. 188.)

Students of other invertebrate groups have insisted on the distinction (*e. g.* Clark (Echinoderms), 1923, and Thompson (Alcyonaria), 1923). It is, however, somewhat difficult to form an idea of the degree of distinction between the two areas. Thompson (*l. c.* p. 53) states that only one-sixth of the South African Alcyonaria lives off both Cape Colony and Natal.

#### *c. North Atlantic and European forms.*

Tomlin (1922, p. 256) has pointed out that the attempt of Sowerby to represent the South African marine fauna as containing a high percentage of European mollusca is not justified by a critical examination of the evidence. He reduced Sowerby's original list of thirty-four species common to South African and European waters to six! I do not know to what extent comparison between European and South African species has been made in other groups. The present collection of Cephalopoda yields five species (or about 15 per cent. of the whole) which range into Northern waters, viz. *Todaropsis eblanae*, *Histioteuthis bonelliana*, *Galiteuthis armata*, *Cranchia scabra*, and *Liocranchia reinhardti*, of which the second and third are found in the Mediterranean. I am inclined, on the whole, to support Clark (*l. c.*) in his contention that the abyssal forms of the South African fauna are probably of North-Western origin. With regard to the deep-water Polypoda and species of *Cirroteuthis*, I certainly consider them to be most closely related to North Atlantic forms, though it must be admitted that we know very little concerning the evolution of these animals.

#### *d. Cosmopolitan forms.*

Many critical species of Cephalopoda are known from only a few examples, and in all probability specific identifications will be largely revised as time goes on. Generalizations about their distribution are therefore at present very unsatisfactory. It is, however, desirable to point out that the hydrographical barrier under discussion has been surmounted by at least seven cosmopolitan species of Egopsida. Whether these forms owe

their wide distribution to the fact that being pelagic and living at the surface they are carried about by surface currents, or whether they are less susceptible to changes in salinity and temperature, we do not know, though we may suspect that the former is the case. It is to be noted that the currents of the North Atlantic have not imposed a very stringent bar to the passage of Cephalopoda, although there are distinct North and South equatorial circulations. Many Egopsida range from the North into the South Atlantic, and we must assume that the currents are not so clearly separated in direction and physical conditions as in the case of the Benguela and Mozambique currents.

#### IV. ADAPTATION OF THE DEEP-WATER POLYPODA.

As we have already noted, a rich fauna of deep-water and abyssal Polypoda was discovered on Dr. Gilchrist's cruises. *Benthoctopus* and *Bathypolypus* are both represented and probably three species of *Cirroteuthis*. The peculiar adaptation of these forms, the structure of several of which has been already carefully studied (Ebersbach, 1915; Meyer, 1906), will be the subject of a separate memoir. It may be pointed out, however, that among the structural peculiarities of these animals is a marked reduction of the pallial aperture, which is noticeable in *Benthoctopus* and reaches its maximum in certain forms of *Cirroteuthis*, in which the aperture is reduced to a small pore. Two very interesting questions arising from this fact may be indicated. In the first case, the respiratory current must be very much restricted. In this connection we may notice that the size and number of the gill lamellæ is often very much reduced (e.g. eight instead of eleven in *C. gilchristi*, three only in *Opiatoteuthis depressa* (Meyer, 1906, p. 216)). Secondly, the original mechanism of locomotion must be modified by the restriction of the amount of water admitted into the pallial cavity, for in several forms the pallial aperture being practically continuous with the funnel-aperture, the only water admitted must be that drawn in through the latter, which (e.g. *C. gilchristi*) is often very minute.

I have to thank Dr. Gilchrist for much personal information concerning this collection, and I would like to express my admiration for the care taken by him in preserving the specimens. My thanks are due to the Survey Committee for permission to publish the results of this study in England, and to Miss Anne L. Massy for valuable information and advice.

The type-specimens described herein are deposited in the Zoological Department of the British Museum. Records of Station, depth, etc., when not given in the text, will be found in the preliminary reports, and are based on Dr. Gilchrist's Reports (Fisheries and Marine Biological Survey, Union of South Africa,

1921-1922). In the summary of local distribution given under each species, the areas from which the specimens were obtained are given as "Cape Town" and "Natal." For the precise location of each station the reader is referred to the above-mentioned report.

## V. TAXONOMY.

### Family ONYCHOTEUTHIDÆ.

#### MOROTEUTHIS sp. A.

One adult specimen (♀) from Stn. 530 (Cape Town); 135 fms.

#### Dimensions.—

Length of mantle (ventral surface);	55.8 cm.
Width " " (aperture);	9.8 "
" " " (maximum);	11.5 "
" across both fins;	30.0 "
" " a single fin;	14.2 "
Length of a single fin;	39.0 "
Length of 1st arm;	{ R. — L. 34 cm.
" " 2nd "	{ R. 37 " L. 40 "
" " 3rd "	{ R. 39 " L. —
" " 4th "	{ R. 43 " L. 42 "
" " tentacle;	91.8 "

*Mantle*.—The specimen is in a relaxed condition, and it is very difficult to be certain as to the shape. There would appear to be a very slight swelling of the visceral sac at the anterior third. It would thus be, in Ishakawa and Wakiya's term, "retort-shaped" (1914, p. 456) and like *M. lönnbergii*. The mantle is five times as long as its breadth, as in *M. robusta*. It is covered dorsally and ventrally with irregularly circular elevations of the mantle, which are sometimes elongated in the antero-posterior axis. The head, arms, and posterior half of the mantle are smooth. The character of these elevations resembles those of *ingens* in being partly circular and those of *lönnbergii* in the longitudinal extension.

*The fins* are rhomboidal, with the posterior end very much attenuated. The antero-lateral margins are half as long as the posterior lateral margins, thereby agreeing with *M. robusta*. The free anterior portion of the fins measures about 35 mm. along the interior border. The fins occupy nearly 71 per cent. of the total mantle length, which far exceeds the corresponding figure in the other species. *M. ingens*, in which it reaches 58 per cent., comes nearest to sp. A in this respect. The breadth of the fins expressed as a percentage of the mantle-length is 54 per cent., which is near the maximum figure given for *M. lönnbergii*.

*The neck-folds.*—The posterior fold has its dorsal portion more or less vertical and its ventral portion transverse, the median and anterior folds have their dorsal parts transverse, the ventral parts oblique.

*The arms.*—The second and third arms are nearly equal in length. The first is definitely shorter than the second and third, and the fourth definitely longer. This condition is equivalent to that found in *M. robusta*. The fixing-apparatus consists of ten or eleven suckers, as in *robusta*. The hooks on the "hand" portion of the tentacle number fourteen pairs. The condition in *lönnerbergii* and *ingens* is transgressive, one having thirteen the other thirteen to sixteen, so that this form therefore resembles *ingens*. The pairs of hooks are arranged diagonally as usual, and the sixth to the ninth pairs are the largest. The apical groups of suckers number thirteen and fifteen, in which it agrees with *ingens*, though again the figures for *ingens* and *lönnerbergii* are transgressive. The tentacles of *M. equatoriulis* are unknown (Thiele, 1921, p. 442).

The preservation of the arms is not very satisfactory, but the following facts can be satisfactorily ascertained:—

There is a faint trace of a dorso-lateral membrane on the dorsal arms and a fairly well-developed frilled "Schutzsaum" on the ventral edge.

On the second arms there are more definite traces of a carina on the ventro-lateral edge. The third arms have a well-developed median carina, which is most obvious along the median portion of the arms. The fourth arms have well-developed membranes along their dorso-lateral margins. Schutzsäume are present on all the arms, but they decrease in size from the first pair onwards and are very rudimentary on the fourth pair.

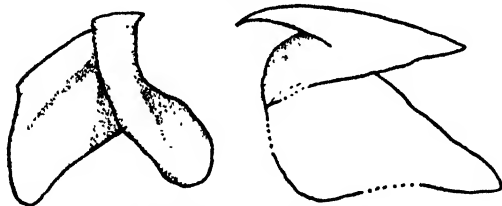
*The gladius* presents some characteristic features. The anterior extremity seems to be pointed, though it is not very well preserved. Two strongly-marked admedian ribs enclose the median area, which exhibits a poorly-developed median rib. The marginal areas commence at about 6.5 cm. from the anterior extremity and widen gradually, attaining their maximum width (1.6 cm.) at about two-fifths of the way towards the other extremity. They then converge again, and gradually get narrower till their outer margins coalesce at some 14.7 cm. from the aboral end. The outer edges of the marginal areas are at first thin, but gradually they thicken to form the outer ribs, which first are visible at about 19.0 cm. from the oral extremity. So far the gladius is not unlike that of *M. ingens* (Pfeffer, 1912, pl. 12), differing from that of *M. robusta* (Verrill, 1879, pl. xxiii, figs. 4-5) in the convergence of the admedian and lateral ribs. The cone measures slightly under one-quarter the length of the whole gladius, and is therefore much larger than that of *ingens* (about one-eighth the size of the gladius) and smaller than that of *robusta* (between one-half and one-third the length of the gladius). The size of the cone relatively to that of the total

gladius of *lönnerbergii* and *equatorialis* are not given. The cone is markedly triangular in section and unlike that of *equatorialis*. The maximum diameter (dorso-ventral) is 1.7 cm.; its maximum width is .9 cm. The shape of the cone seems to approximate to that of *M. lönnerbergii*. The cone of *robusta* is described as circular, which differentiates it at once from the other three forms.

The *funnel cartilages* are long and narrow. They are asymmetrically developed in this specimen and are not in a fit condition for description.

The *mandibles* (text-fig. 1) are very characteristic. They differ from those of *M. robusta* (Verrill, 1879, pl. xxiv.) and *ingens* (Brit. Museum) in the considerable posterior extension of the upper rostrum\*, a feature in which it resembles *Architeuthis* (Verrill, l. c. pl. xviii.). The inferior mandible resembles those of *robusta*, *ingens* (as figured by Smith), and *Architeuthis* in the great depth of the gular lamina. A special feature, possibly found in *ingens* and *robusta*, and certainly occurring in *Architeuthis*, is the presence of a marked lateral rib on this lamina (cf. Joubin, 1900, pl. xiv.).

Text-figure 1.



*Moroteuthis A.* Mandibles.

The lateral walls of the mouth are, as in *Architeuthis*, furnished with a strong cuticular membrane which is beset with strong teeth. These are irregularly arranged, vary in size, and are more or less curved in shape. Their irregular granules observed by Verrill (1879, p. 205) in *A. princeps* were not found.

The *radula*.—Our knowledge of this organ in *Moroteuthis* is limited to a slight description and a poor drawing in Smith's description (1881) of *ingens*, Verrill's (*loc. cit.*) description of *robusta*, and that of *equatorialis* given by Thiele (1921). Smith's account is too general for taxonomic purposes. A comparison of the radula of this form (text-fig. 2) with those of *equatorialis*, *robusta*, and *ingens* (Brit. Mus.) reveals at once marked difference in all the teeth. The prominent lateral cusps on the wide basal plate of the rhachidian tooth and the widely-set and prominent main cusp of the first lateral are the most marked differences.

I should draw attention to the fact that Lönnerberg (1899,

\* For terminology used, cf. Meyer, 1913, fig. 25.



pp. 59-60) has investigated the structure of the dermal papillæ in *M. ingens*, and has concluded that they are at once an arrangement of adaptation with regard to hydrostatic pressure and an accommodation for the reserve of oily fat with which the skin of this squid is so richly endowed.

Text-figure 2.



*Moroteuthis A.* Radula. X 22.

*Relationships.*—Ishakawa and Wakiya (1914, p. 456) have given a table in which the differentia of *robusta*, *ingens*, and *lönnerbergii* are set forth. By a comparison of the available data and the addition of fresh evidence we may distribute the principal features of the Cape form as follows:—

Resembles *lönnerbergii* in 3 characters.

“ *robusta* “ 4 “  
 “ *ingens* “ 5 “

Intermediate between *ingens* and *robusta* in 1 character.

Unique in 1 character.

It will be remembered that in some cases the same information is not available about the three species with which we are comparing our form. For this reason a comparison with Thiele's *equatorialis*, of which the tentacles are unknown, is given separately. From this equatorial Atlantic species the Cape form is strangely different. Comparison between the two shows that the following characters are markedly dissimilar:—Skin, fins (relative length of margin and total length relative to that of the mantle), the form of the visceral sac, the structure of the cone of the gladius, the radula, and even the mandibles.

In any case there is no preponderating tendency in the resemblances shown by this form, if we bear in mind that in one at least of the characters resembling *ingens* (the size-ratio of the fin to the mantle) the resemblance is only a relative one, and that in two of the others the character in question is transgressive as between *ingens* and *lönnerbergii*. It should also be noted that there are significant differences in the radula and mandible from *robusta* and *ingens*. I think we should discard any notion of special affinity, with possibly a reservation that there is a slight

tendency towards *ingens*. At present *lönnerbergii* is known only from Sagami Bay (Japan), *robusta* from Alaska, *equatorialis* from mid-Atlantic, while *ingens* is recorded from several localities in Patagonia and Magellan Straits and from the South Orkneys (Hoyle, 1912) and New Zealand (Massy, 1916, p. 165). The genus may therefore be regarded as practically cosmopolitan, while this element in the Cape marine fauna is, as far as our knowledge goes, possibly of Southern origin. Although our data for comparison with other forms is not very complete, I consider we know enough to assume that this form is specifically different. I do not consider, however, that a single specimen is enough material upon which to base a specific definition, especially as the form in question exhibits some vague affinities with other species.

? *LYCOTEUTHIS* sp.

One adult example (? sex) from Station 156 (Natal); 324 fathoms.

This interesting form is in a very fragmentary condition, lacking the eyes and part of the head, the tentacles, the skin of the mantle, and being otherwise in a very poor condition.

In the absence of the tentacles it is very hard to assign it a position in the system proposed by Pfeffer, and even the generic position is doubtful.

The following characters agree with those of *Lycoteuthis* :—

- (1) The presence of circumanal and branchial light-organs ("analoganen" and "ventralorganen");
- (2) the shape of the funnel organ;
- (3) the presence of a valve in the funnel;
- (4) the general bodily shape;
- (5) the general shape of the gladius (text-fig. 3), in which the lateral area expands about half-way down the gladius, contracts and expands again at the extremity. In this form, however, the apical expansion is much broader than in *Lycoteuthis*.
- (6) The buccal membrane (cf. Pfeffer, 1912, pl. xiv. fig. 3).

The following structures do not resemble those of *Lycoteuthis* :—

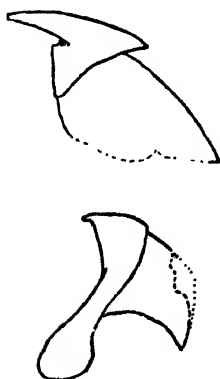
- (1) The mandibles (text-fig. 4; cf. Chun, 1910, pl. iii. fig. 3);
- (2) the radula (text-fig. 5; cf. l. c. fig. 15);
- (3) the suckers of the arms have a single armature of teeth (well marked on the distal edge), the inner teeth of *Lycoteuthis* being absent;
- (4) the ocular light-organs found in *Lycoteuthis* are probably absent.

Chun's specimens of *L. (Thaumatolampas) diadema* came from South Africa (off Cape Town). Of Pfeffer's examples, one is from Western America, one from the Atlantic (?), and one from

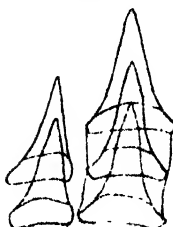
Text-figure 3.

*Lycoteuthis* sp. Gladius. Slightly reduced.

Text-figure 4.

*Lycoteuthis* sp. Mandibles.  
× 275.

Text-figure 5.

*Lycoteuthis* sp. Radula, median teeth.  
× 35.

Australian waters. Two of Pfeffer's specimens are from the stomach-contents of marine vertebrate carnivora, and the third is a mangled specimen. It is probable that the specimen under discussion was likewise voided by a large carnivore. With this proviso, we may note that the genus is apparently widely distributed.

### Family ENOPLOTEUTHIDÆ.

*ABRALIA GILCHRISTI* Robson. (Plate I. fig. 1.)

*A. gilchristi* Robson (1924 b).

1. One specimen (♂) from Station 81; 280 fathoms.

2. " " (♂) " " 48; 240 " "

The above are cotypes.

Although in one or two respects these animals do not seem to have assumed the final adult form, the differences from the adult are so slight that the specimens are regarded as suitable for description. The animals are sexually mature, with well-developed gonad and spermatophores.

<i>Dimensions</i> (in mm.).—		1.	2.
Length of mantle;		40	40 (damaged).
Width of mantle-aperture;		12.5	15
" " visceral sac (across maximum width of fins);		8	7.5
Fins, max. length;		32	32
" " width (total);		32	31 ± 2
Head, diameter;		15	11
Tentacles, length;	{ L.	46	Damaged.
	{ R.	52	
Arms: 1, " ;	{ L.	26	28
	{ R.	27	—
" 2, " ;	{ L.	27	29.5
	{ R.	28.5	29.5
" 3, " ;	{ L.	25	30
	{ R.	27	31
" 4, " ;	{ L.	34	35
	{ R.	36	33

The mantle-aperture is flanged outwards\* as in the young stage of *A. morisii* (Chun, 1910, pl. vi.). The other species, notably *A. hoylei* and *pfefferi*, differ markedly in this respect. The width of the mantle-aperture is, however, relatively far more accentuated in *A. gilchristi* by reason of the slender, tapering visceral sac.

A very characteristic feature in which this species differs from *morisii* and the other species is the great length of the fins relatively to the mantle and the marked disparity in their

\* This is not very apparent in the photograph (Pl. I. fig. 1), which was taken after dissection.

anterior and posterior borders. The greatest width across the fins lies at the anterior third, in which they tend to agree with *pfefferi*. The anterior margin is convex, the posterior concave as in *hoylei*.

The distal part of the tentacle has been fully described. It is unlike that of *pfefferi*. The tentacle-extremity in *A. hoylei* is not properly known, while that of *A. morisii* was but scantily described. From the figure (Chun, *l. c.* pl. viii. fig. 4), however, it differs somewhat markedly from that of *gilchristi* in that the sucker-bearing area is slender and elongate, while in the latter form it is short and compact; and the suckers are arranged in close, even rows instead of being irregularly scattered. The median portion of the "hand" consists of two rhachidian rows of hooks, of which there are four large posterior ones and four small anterior ones. The hooks are still partly encased in a fleshy sheath. This condition, which may be a juvenile trait, is nevertheless found in adult stages, such as *hoylei* (Pfeffer, *l. c.* fig. 9, pl. 17, and Joubin, 1896, fig. 9, p. 30). Remnants of the anterior marginal row of suckers are found as in *morisii*. This consists of a row of minute suckers, one between each pair of anterior hooks and 2-3 suckers just abreast of the most distal hook. The carpal part of the tentacle consists of an adhesive pad of 4-5 (not 5-6 as originally stated) suckers and an uncertain number of corresponding knobs. In the number of suckers *gilchristi* agrees with *hoylei* and *morisii*, though it is very doubtful whether the number is of diagnostic value.

The tentacle club is furnished with a very well-developed membrane on the anterior edge, extending from the 2nd to 3rd hook and rapidly expanding until it is as wide as the tentacle itself. This membrane is either absent or but very poorly developed in the allied species. There is a short proximal membrane extending from the adhesive pad to beyond the first hook.

### *The Arms.*

First pair. The carina is well developed distally and extends about two-thirds to half-way from the distal extremity. The "Schutzsäume" are developed as lappets, those on the ventral side being far better developed than those on the dorsal. There are 10-11 pairs of hooks, which gradually become more diagonally disposed and are continued by some 5-6 linearly arranged ones.

Second pair. The carina occupies less space than in the first pair. The lappets of the dorsal "Schutzsaum" which is the better developed of the two, tend to become linked up by a continuous membrane. There are ten to twelve pairs of hooks followed by a varying number of single suckers.

Third pair. The carina attains its maximum development. The dorsal "Schutzsaum" is almost entirely absent, the other being less well developed than in the other arms, though the lappets are still perceptible in some cases.

The linear arrangement of suckers commences further down the arm, viz. after the 6th to 8th sucker. The hooks do not appear till some 10 mm. from the proximal end of the arm.

Fourth pair. The carina is represented by a low ridge (not "kräftig entwickelt" as in *morisii*) on the posterior angle of the arm. This is continuous all the way down the arm and passes round the base of the third arm. The "Schutzsaum" is represented by low lappets on each side. There are some 8 paired hooks and 6-8 unpaired ones. In specimen No. 1 the right arm has the ventral "Schutzsaum" much expanded at the extremity of the arm; the dorsal "Schutzsaum" is similarly expanded, but not so much as its fellow. There is no trace of this on the left arm. The same condition is found in specimen No. 2, though in that case the left arm is damaged. It is conceivable that this expansion is the hectocotylus, but according to the description of Chun (1910, p. 82) the fourth *left* arm is modified and the resulting structure is very much more elaborate.

On all the first three pairs there are distal patches of suckers biserially arranged. On the third pair some 15-16 pairs are found.

The terminal organs of the 4th arms are individual in shape in that the main bulbs are longer than in the other species and that there are four smaller end-bulbs. The basal support is likewise deeper than in the other forms.

*The light-organs.*—Those on the ventral mantle are massed on each side of a narrow bare strip which occupies the median line. There is no trace of seriation in these masses. There are three streaks of light-organs on each side of the funnel. On the head and arms the arrangement is as follows:—

(a) Two median ventral rows separated by a narrow median bare area, down the centre of which is a sparse row. These ventral rows are continued up the posterior side of the fourth arms.

(b) Posterior and anterior gular patches joined by two more or less parallel subocular rows. The anterior gular patch sends two rows up the anterior side of the fourth arms.

(c) A circumocular series.

(d) Possibly arising from (c), a double row passes up the third arms, one strip on each side of the carina. This general plan differs from that seen in the other species. The series in *morisii* and *pfefferi* are less well developed, while the plan of arrangement differs in *hoylei*.

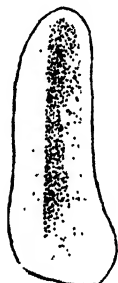
*The adhesive organs* (text-fig. 6) are different from those described in the other species, the groove of the cephalic plate being more median in *hoylei* and *pfefferi*, and the whole plate being much longer and thinner in *morisii*.

*The reproductive organs* (text-fig. 7).—Both examples were males with well-developed testis and fully-formed spermatophores.

The male organs have been described for *A. morisii* by Chun (1910, pls. ix.-x.), but there are certain features in this species requiring notice.

The *vas deferens* and the first two sections of the *vesicula seminalis* more or less correspond with those of *morisii*; but the latter organs in this species are placed on opposite sides of the communication with the third section of the vesicula. The latter resembles that of *morisii*, but the proximal part of the *vas deferens* is more clearly differentiated, thinner and longer, and terminates in a very slender junction with the prostate. The junction of the *vas deferens* with Needham's organ is very much lower down in this form. The appendix of the prostate and ciliated canal resemble those of *morisii*. The prostate itself differs markedly in form from that of the latter. Needham's organ is blunt-ended, and the penis is abruptly differentiated from it in size. Needham's organ was found completely full of spermatophores, and the *vas deferens* in each

Text-figure 6.



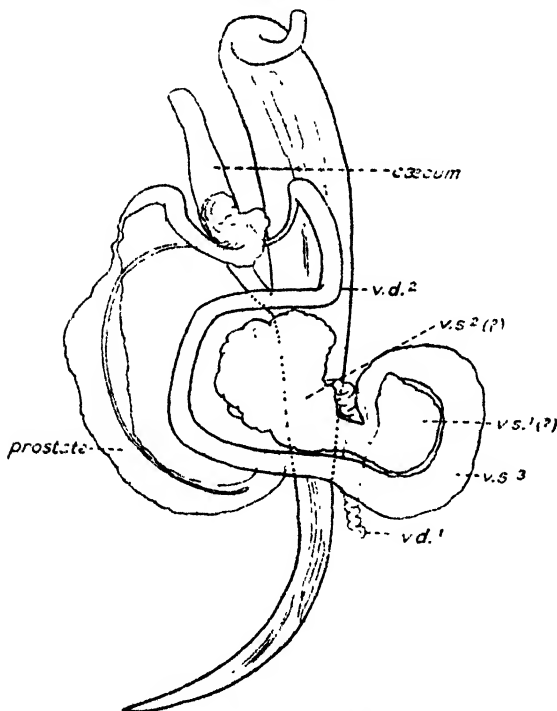
*Abralia gilchristi*. Adhesive organ.  $\times 6$ .

case contained a spermatophore, which, with those in Needham's organ, had their aboral poles directed proximally. Nothing was observed which threw light on the question (*cf.* Chun, 1910, p. 93) as to how the spermatophores attain their final position in Needham's organ, but I was fortunate enough to find one in the cæcum of the prostate doubled on itself, which suggests that some change of position may be effected in that organ.

*Affinities, etc.*—As we have already stated, these forms are sexually mature, and therefore deserving of description. An interesting point arises, however, in that, though mature, they still exhibit a feature which, according to Pfeffer's Key (1912, pp. 149-159), would justify their inclusion in his "*Micrurhalia*" larval stage. The marginal row of anterior suckers is still present on the tentacle; moreover, the hooks are still encased in fleshy sheaths, which is apparently a juvenile character, as it is found in the *Compsoteuthis*-stage (*cf.* Issel, 1908, pl. ix, fig. 17). Nevertheless this condition is found (*v. supra*) in the mature

*hoylei*. The bulk of the evidence from structure alone is decidedly in favour of these specimens going into *Abralia* (s.s.), while the line between *Microbralia* and *Abralia* is obviously impossible to maintain in all cases. The only conclusion to draw is that the persistence of the marginal anterior suckers into sexual maturity is of no taxonomic value, being merely an instance of the persistence into sexual maturity of structures which are lost in other forms.

Text-figure 7.

*Abralia gilchristi*; ♂ genitalia.  $\times 47$ .

v.s. 1-3, seminal vesicle. v.d. 1-2, vas deferens.

Mature forms of *Abralia* (s.s.) are known from the Mascarenes (*A. hoylei*), the Mediterranean (*A. pfefferi*), the Red Sea (*A. steindachneri* Weindl, 1912), Hawaii (*A. trigonura* Berry, 1913; *astrosticta*, id. 1909), the Kermadec Is. (*A. atrolineata*, id. 1914), and E. and W. Africa (*A. (Abraliopsis) morisii* Chun—not Vérany—1910). As *A. morisii* is found both in the Gulf of Guinea and off the East Coast, it is not surprising that our form exhibits the more marked affinity with that form. It likewise



shares several features in common with *A. hoylei*. It is impossible, however, to ignore the fact that this form differs in many substantial details from *morisii* (e. g. general form, tentacles, locking apparatus, genitalia, hectocotylus), and that these details cannot be attributed to age, so that, in spite of the distribution of *morisii*, one can do nothing less than accord this form specific rank. It may be regarded as one of a group of three species which up to the present are confined to the Equatorial and Southern waters of the Indian and Atlantic Oceans (v. p. 622).

### Sub-family OCTOPODOTEUTHINÆ.

#### OCTOPODOTEUTHOPSIS sp. (Plate I. fig. 2.)

One example (? sex) from Station 347 (Cape Town); 900 fathoms on ooze.

#### Dimensions.—

Mantle, max. length, dorsal;	13.5 mm.
"    "    "    ventral;	13    "
"    "    width;	7.5 ± 1 mm.
Fins, max. length;	13 mm.
"    "    width;	10    "
Width across both fins;	23    "
Length of head (base of first arms to mantle-edge);	7    "
	L.                    R.
Arms: 1, length;	—                    —
"    2,    "	19 mm.            21 mm.
"    3,    "	18    "            —
"    4,    "	—                    11    "

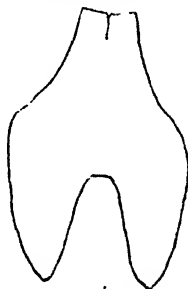
The ground-colour (spirit specimen) is pale livid, and the surface of the arms, head, and mantle is sparsely covered with reddish-black chromatophores. The specimen is in rather poor condition, the arms especially being very much damaged.

The *arms* are drawn out into fine extremities and lack the "end swelling" found in *Octopodoteuthis*. They all appear to be cylindrical. Only a few suckers remain, but it is possible to make out their structure fairly well. They are widely spaced, do not overlap, and are arranged alternately on either side of the marked ventral furrow. They give rise to small hooks, the points of which are scarcely reflected and their bases are large and fleshy. There do not appear to be any distal unmodified suckers as in *Octopodoteuthis*. The tentacles are completely absent. The fins are remarkably large. They are longer than wide, being conterminous with the mantle. Posteriorly on the dorsal surface they seem to project beyond the extremity of the body, but on the ventral surface this is seen to be due to a slight reflection of the extremity of the mantle and the fin insertion with it.

The *head* is large and prominent. The funnel is short and stout. It is provided with a well-developed funnel organ (text-fig. 8), of which the exact shape of the median piece only could be studied adequately. The articulatory cartilages are in too poor a condition to make out satisfactorily.

Although the fins and arms seem to be well developed, it is possible that this form is not mature. The reproductive organs could not be found, but imperfect preservation may be responsible for this. Doubt as to its age and the poor condition render a

Text-figure 8.



*Octopodoteuthopsis* sp. Central plate of funnel organ.  $\times 11$ .

description and determination very undesirable. On the other hand, it is obvious that the specimen occupies a rather unique position. The characters that are not rendered *sub judice* owing to the uncertain age seem to suggest that it may either occupy a separate generic position in Pfeffer's section B (1912, p. 124) of equal value to *Cuciteuthis* and *Octopodoteuthopsis*, or else be an aberrant and undeveloped form of the latter.

The characters in which it agrees with the latter are:—

- (1) The widely-spaced suckers;
- (2) the broad bases of the latter;
- (3) their alternating arrangement;
- (4) the ventral furrow on the arms;
- (5) the complete disappearance of the tentacles.

It differs from *Octopodoteuthopsis* in the completely terminal position of the fins and in size.

This genus is at present represented only by *O. megaptera* Verrill, a rather imperfectly-described form from the New England coast (707 fathoms), from which the Cape form differs not only in the characters detailed above, but in the shape of the fins.

Like the preceding species, these forms are evidently favourite food of marine carnivora. Verrill's single specimen was very badly mutilated. The allied genus *Cuciteuthis* is likewise known mainly from fragments or stomach-contents of whales.

## Family HISTIOTEUTHIDÆ.

*HISTIOTEUTHIS BONELLIANA* (Fér.).

A. 1 example (♂) from Stn. 542; 958 fms.

B. 1 " (♀) " " 343; 470 "

Although this species has been very carefully described by Pfeffer, it is desirable to add some fresh data from this material.

*Dimensions.*—

	Specimen A.	Specimen B.
Arm formula;	3. 2. 4. 1.	3. 2. 4. 1.
Total length to tip of arms;	182 mm.	245 mm.
Mantle, length;	46 "	67 ± 2 mm.
Fin, length;	22 "	27 mm.
" breadth;	33 "	37 ± 2 mm.
Fin, length in per cent.		
of mantle length;	47 %	46 %
" breadth in per cent.		
of mantle length;	71 %	55 %

The general shape of the mantle differs somewhat from that usually recorded. In specimen A it diminishes in width very gradually towards the apex, and the sides are less abruptly convergent than is usually seen. The apex is very blunt and there is no point or frenulum (*cf.* Pfeffer, 1912, p. 298). Specimen B, which is a little distorted, is even more unlike the usual form. The maximum width is not at the mantle-aperture but just above it, and the sides are markedly convex. On the other hand, the extremity is pointed in specimen B, and there is a suggestion of a frenulum.

The fins are of the same general shape as that figured by Pfeffer; but in both examples they are shorter in relation to the total mantle-length than the average shown in Pfeffer's table (1912, pp. 318-319). The lappet formed by the projection of the anterior edge beyond the point of junction with the mantle is not so large as in Pfeffer's description.

The head is exceptionally large in specimen A. In specimen B it is distorted. In the former it would appear (if we make due allowance for the asymmetry) to have been actually wider than the mantle-opening. With a similar allowance for the asymmetry the head seems to be more rectangular than usual. The line of junction with the "neck" is marked by a non-pigmented scarcely perceptible ridge ("Halskante"), which has a well-marked indentation on the ventral surface. The eyes are markedly asymmetrical. The left-hand aperture is more than twice as large as the right-hand one. The left-hand eyes themselves are larger, and, in addition, in both specimens the lenses are found protruding from their sockets. The circumocular light-organs of this side are ill-developed, as in other specimens. This asymmetry is found in

others members of this family (cf. *Meleagroteuthis* Berry, 1910, pp. 305-308), and is regarded by Pfeffer as a family characteristic. It is also found in the Polypod *Cirrotheuthis macrops* Berry, *l. c.* p. 274. The fact that an eye has been torn or partly torn from its socket in both my specimens, as is similarly noted by Berry, is, I think, accidental. The reduction of the circumoral light-organs and the length of the arms of the left side (noted by Pfeffer, *l. c.*) seem to indicate a more deeply-seated asymmetry.

The oral membrane has been withdrawn very considerably owing to contraction, and cannot therefore be very satisfactorily compared with Pfeffer's account. Nevertheless, the structure of the outer membrane is remarkably different from that figured in the latter. There is a single muscular "support" between the first and second arms, one each approximately over the third arms, and one corresponding to each of the fourth arms. I am assuming that I am correct in considering that the inner membrane with its six supports has contracted inwards, leaving exposed the outer one figured by Pfeffer which has indeed seven supports, but in a different position.

*The arms.*—Even in the better-preserved specimens the surface-tissues are in poor condition, so that it is difficult to make certain about the occurrence of the carina. There is a short yellow-coloured membrane on the third pair towards the distal end. I am of opinion that the other fins described by Pfeffer were not present in the living animal. The external keel ("Ausserkante") of the fourth arms is barely appreciable in specimen A, better marked in B, though it cannot be described as "saumartige" (Pfeffer, *l. c.* p. 301). The terminal light-organs have been fully described by Hoffman and Grimpe (1921, p. 201). In specimen A they measure some 13-14 mm., and are, as usual, confined to the three upper-arm pairs.

*The suckers* are well seen in specimen A. On the first pair of arms (hectocotylized) they are widely spaced over the part of the arm conterminous with the velum, and moderate in size. At the top of the velum they rapidly increase in size. Four pairs (6-10) are very large; then there is a rapid decrease in size, and the suckers become close and numerous, but they are arranged in two rows, not in four as Chun states for his examples (1910, p. 168, text-fig. 1). On the first three pairs they are very widely spaced to start with, the usual interval being 6 mm., or over twice the size of the suckers themselves.

On the ventral pair the proximal suckers, which begin much further away from the base of the arms (some 20 mm.), are all small and apparently somewhat obsolescent.

The suckers correspond with the description given by Pfeffer. The reduced suckers of the fourth arms are denticulated.

The tentacles differ somewhat from the standard description, especially in the more expanded distal area of the club, which bears more numerous suckers (viz. series of 7, 6, 5, 4, etc., each instead of 4, 3, etc.), and in the persistence of an additional

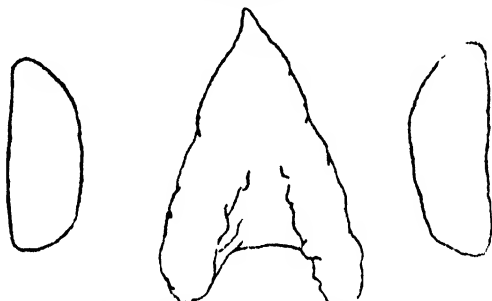
marginal row of very small suckers. The tentacular fin is not so well developed nor is the extremity so finely drawn out, as in Pfeffer's specimens.

#### ANATOMY.

The gladius, mandibles and radula, pallial complex and digestive system, and male and female genitalia have been described in part already, while the position of *Histioteuthis* has been discussed from this standpoint by Chun (1906, p. 743).

The funnel organ has been incompletely figured by Weiss (1889, p. 84). There is in this case (text-fig. 9) two simple lateral

Text-figure 9.



*Histioteuthis bonelliana*. Funnel organ.  $\times 16$ .

plates, which in the more adult specimen (B) have their outward side straight and the inner side curved. The median plate is triangular, its inferior angles being somewhat prolonged. In the larger specimen its surface is very much folded.

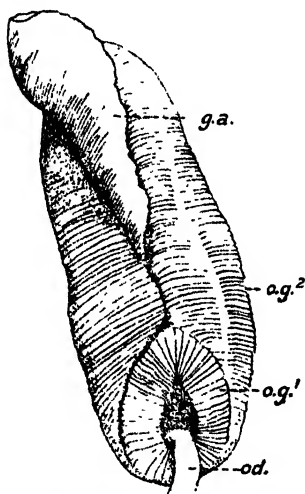
#### Reproductive System.

The female organs have been somewhat scantily described by Weiss (*l. c.* p. 84).

On opening the visceral sac the large oviducal and nidamentary glands are conspicuous objects. The fertile ovary extends downwards over the heart and other viscera. The oviducts leave the capsule of the ovary in a dorsal position, and run downwards (in specimen B) as somewhat flattened ducts. They expand on a level with the gills to form the oviducal glands (text-fig. 10). The latter are subcircular rings of folded glandular tissue, with a large central orifice through which the oviduct passes. In general structure they resemble those of *Thysanoteuthis* (Brock, 1882, pl. xxxiv. fig. 3). They are not, however, free of the folded glandular distal part of the oviduct, but are implanted in it at the base. I cannot follow Brock in calling the subsequent glandular portion "oviduct," as it is highly probable that it fulfils a special glandular function. I have therefore named the original

gland and the distal, larger part the first and second oviducal glands respectively. A glandular appendage connected with the latter was found at the extremity of the oviducal apparatus. It was somewhat damaged, so that it is uncertain if it is a separate organ or merely part of the second oviducal gland. The nidamentalary glands are larger and more solid than in Weiss's figure. They are two-thirds the size of the oviducal glands. In general

Text-figure 10.

*Histiotenthis bonelliana*. Oviducal gland.

od., oviduct; o.g., o.g.2, oviducal glands; g.a., glandular appendage.  $\times 3$ .

shape and fine structure they are, as Weiss points out, extraordinarily like the oviducal glands, even to the deeply-excavated fold which constitutes the characteristic oviducal aperture. The question indeed presents itself whether they may not be morphologically the rudiments of a second pair of oviducts.

As in *Thysanotenthis*, the oviducts proper become thicker and more convoluted in the middle of their course.

### Male System.

The accessory glands were quite large, and Needham's organ contained spermatophores (text-fig. 11). The testis, however, was in a very undeveloped condition.

The figure of the closely-allied *Callitenthis* given by Chun (1906, fig. 5) shows remarkable bilateral symmetrical male organs. This condition is not found in the present genus. Neither Chun nor Weiss figure the male genitalia of the latter. The usual three accessory glands of the vas deferens are present; the ciliated canal,

prostate, and appendix of the latter are present. Needham's organ is very slender and very long, extending to the extremity of the visceral cavity. It contains spermatophores of the type figured (text-fig. 11). The sperm-plug is very short compared with that of *Calliteuthis* (Chun, 1910, pl. xx. fig. 8), and may be an indication of immature condition. The spermatophores are otherwise completely developed.

Text-figure 11.



*Histiotentus bonelliana*. Spermatophore.  $\times 1975$ .

The complete development of the secondary sexual organs (? exclusive of the hectocotylus) is in startling contrast with the fact that the testis was found to be in a very rudimentary condition, present only, in fact, as a thin strip of tissue 2-3 mm. long. The physiological significance of this and its bearing on the problem of the development of the secondary sexual organs will be discussed elsewhere.

### *The Alimentary System.*

The mandibles differ from those figured by Verrill (1879, pl. xxvii. fig. 4, *H. collinsii* = *bonelliana*). The rostrum of the upper mandible is not markedly curved as in Verrill's figures, but nearly straight, becoming curved only at the tip. Nor is the palatal plate so upright. Certain other smaller differences are noticeable. In the lower mandible the top of the rostrum is not curved in the same direction as in Verrill's figure, while the rostral laminae are more expanded. The figure of the mandibles given by Férussac (1835, pl. lxvi. fig. 6) agrees partly with Verrill's figure and partly with the Cape form.

The radula has been figured by Verrill (1879, pl. xxxvii. fig. 5) and by Thiele (1921, pl. liv. fig. 21). Verrill's figure is unsatisfactory, as it does not agree with the text (*l. c.* p. 237). Comparison with Thiele's figure renders it possible that in this organ at least the Cape form shows certain differences of a varietal nature. The median tooth is more or less similar in both cases. The base and inner edge of the admedians differ. The laterals are similar; while the marginals (in a very carefully extracted and mounted specimen) are entirely wanting.

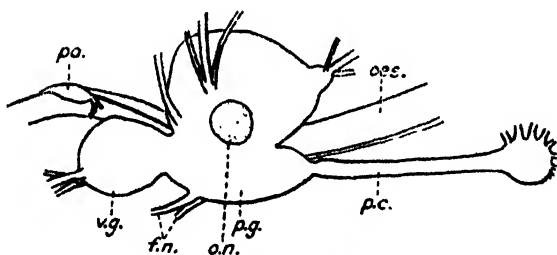
The oesophagus is long and exceedingly slender. Posteriorly to the cephalic cartilage it is as narrow as the (double) visceral

nerve. The stomach is dark purplish brown in external colour and piriform in shape. The cæcum is somewhat lighter in colour and very distinctly spiral. The rectum is stout and receives a very slender duct from the ink-sac. The latter is small and, together with its duct, measures about 14 mm. in length. The salivary ducts are fused together a little below their point of union with the glands.

*Nervous System* (text-fig. 12).

The cerebral, visceral, and pedal ganglia are closely approximate, and may be practically regarded as one mass. The pedo-brachial commissures are fused into a single strong median trunk. The brachial ganglion is separated and at some distance from the other main ganglia. The ganglia are largely encased in the cephalic cartilages. The optic ganglia are very large. A curious asymmetry of the visceral nerve was found. This nerve accompanies the œsophagus and passes through the back of the cephalic cartilage as a single trunk. At this point it divides into two

Text-figure 12.



*Histioteuthis bonelliana*. Central nervous system.

*p.c.*, brachio-pedal connective; *f.n.*, funnel nerve; *o.n.*, optic nerve; *oes.*, œsophagus; *p.g.*, pedal ganglion; *po.*, parœsophageal ganglion.

branches, and almost at once each branch gives rise to a ganglion: from the left-hand member of this pair a large nerve runs forward with the œsophagus and enters the tissues of the pharynx. A second smaller nerve apparently passes to the visceral ganglion, though the connection could not be made out with absolute certainty on this side. On the right only the connective with the visceral ganglion occurs.

*The cephalic cartilage.*—This is divisible into a more solid median area and two lateral expansions which constitute the eye-sockets. The median portion is saddle-like. Part of the ganglionic complex is covered by it, and it is pierced dorsally by a foramen, through which the œsophagus etc. pass. The lateral expansions are very thin and delicate, and are markedly concave, the concavity being directed ventrally and outwards.



*Distribution.*

This species is well known from numerous localities in the North and South Atlantic, from the Mediterranean, and from one record (Thiele, 1921, p. 452) in the Indian Ocean, south of Madagascar. Certain differences between the specimens recorded are obvious (*e.g.* in the radula and mandible of the previous form); but their taxonomic significance is very uncertain. Their correct interpretation would depend on more plentiful material than is at present available.

## Family OMMATOSTREPHIDÆ.

## TODAROPSIS EHLANÆ (Ball).

9 specimens from Station 9, Cape Town, 100 fms.;	2 ♂, 7 ♀.
5 " " " 7, " 112 "	2 ♂, 3 ♀.
2 " " " 7, " 126 "	both ♂.
1 " " " 44, " 85 "	♂.
3 " " " 54, " 67 "	2 ♂, 1 ♀.
2 " " " 20, " 67 "	1 ♂, 1 ♀.
1 " " " 58, " 104 "	♀.

This form has been very fully described by Pfeffer (*l.c.* p. 423), but, owing to its wide distribution, it is desirable to present such data as may make the relationship of the Northern and Southern forms plain.

*Neck-folds.*—The two halves of the anterior transverse fold vary in their method of contact from a straight line to an angle of some 150°.

The width\* between the transverse ridges also varies considerably. Thus in a large specimen we find it measuring 6 mm., the same as that in a specimen less in size, while in a specimen measuring 89 mm. in mantle-length it measures 3.75, and in one of 84 mm. it is 5 mm. The direction of the longitudinal ridges is uniformly as described by Pfeffer, except that of the third ridge, which varies through about 45°. The malar fold in two specimens is very much reduced and the malar projection (at the dorsul angle of the funnel-fossa) is exaggerated.

The dimensions of the fins are given in Table I. From it we gather that the ratio of the fin-length to that of the mantle is higher on the average than that given by Pfeffer (p. 432), viz. 51 per cent. as compared with 45 per cent. Similarly, the average fin-width ratio is 74, while Pfeffer's figures yield 77 per cent. We have to determine whether these figures are significant.

There is a marked correlation between the fin-length and fin-breadth ratios and the size of the animal, larger specimens

\* This measurement is taken across the admedian dorsal (3rd) longitudinal ridge.

tending to have relatively longer and narrower fins. Whether this is a true age-difference or not it is difficult to say, but in all probability, even on such exiguous numbers as are available, size is a fair index of age. This has been previously commented on by Girard (1890 *passim*, 1891, p. 44). The average length of the mantle of the twenty-one examples from the Cape is 87 mm.; that of Pfeffer's ten examples, for which figures are available, is 89, which we may regard as equivalent.

Whether there is any correlation of these characters with sex it is very hard to say. The females outnumber the males by two to one, while the numbers available are very small. The following table represents the available knowledge:—

TABLE I.

	Mantle-length (mm.).	Fin L. Mantle L.	Mantle-length (mm.).	Fin L. Mantle L.
Pfeffer:	♂ (4).		♀ (5).	
	92	45	86	46
G. C. R.:	♂ (7).		♀ (14).	
	80	51	77	51

It is inadequate for a final judgment, but seems to indicate no particular difference between the sexes. Girard ('90 *a* and *b*) does not refer to any sexual differentiation in this respect.

The arms show very considerable variation in size and relative proportion, both individually and in the opposite sides of the same individual. Thus in nine cases, only two showed the same relative sizes on the right and left sides. It is natural that a structure so liable to injury and modification as the arm-tips should exhibit such variability.

The second arm is usually the largest, but in nine cases three specimens have the second and third equal in size on the left, and three cases (not the same) have the same on the right. The first pair is usually the shortest, but in the same nine cases the fourth is the shortest twice on the left and three times on the right, while the first and fourth are equal twice in both cases.

In assigning the above proportions, cases which are within 3 mm. are regarded as equal.

The data given above are in agreement with Pfeffer's description of North Atlantic material. The first pair has no carina, but the ventral edge of the somewhat quadrangular arm sometimes shows a trace of a membrane (*cf.* Hoyle, 1903, p. 2). The "Schutzsäume" are very well-developed, and do not appear to differ from previous descriptions except that in the latter no mention is made of the fact that the muscular supports of the membrane are prolonged half-way across the arm as "quer Balken," in which the stalks of the suckers are involved. The

second pair corresponds with the previous description, though it may be mentioned that the carina is very well developed in all specimens. As regards the third pair, I find the well-developed carina frequently begins at the arm-base, contrary to Pfeffer's statement (1912, p. 426) that the proximal quarter or fifth is free. The fourth arms have the carina replaced, as Pfeffer states, by an "Ausserkante," but I have found no specimen in which this could be described as "mässige." Contrary also to Pfeffer's description, I find the ventral "Schutzsaum" tends to be somewhat more strongly developed than the dorsal.

*The suckers* of the sessile arms offer some contrast to those previously described. Pfeffer says these suckers are provided with six triangular teeth flanked by a pair of squarish teeth (eight in all). After careful examination of numerous examples, I find nine teeth in all to be the average, while abrupt transition from "triangular" to squarish ("dreieckig" . . . "Zinnenformig") is by no means the rule.

*The tentacles.*—The form and keeling of the shaft resembles that of the Northern form with great constancy. The club in eleven cases was somewhat under the average size given by Pfeffer ("zwei Fünftel oder mehr der Gesamtlänge"). The numbers and grouping of the suckers on the club correspond in detail with Pfeffer's description. Differences of detail, such as the occurrence of three suckers on the left carpus and four on the right, are met with, as well as asymmetry of the large (median) suckers, of which eight pairs occur on the left and seven on the right. I find 22 or 23 a more frequent figure for the distal sucker pairs than 20. The tentacular suckers are furnished with an average of 30 teeth (range 27–33). This is the actual number found in the type-specimen (*cf.* Hoyle, 1903), but it is lower than the figure given by Pfeffer, which is 34. There seems to be no relation between the number of sucker-teeth and age or sex.

*The hectocotylized arm* attains in one specimen the degree of development described by Joubin (1920, p. 59) for a Gulf of Gascony specimen. These are the only two cases known of this extreme degree of differentiation.

The *radula* resembles that figured by Hoyle (1903, pl. i. fig. 6). The figure given by Jatta (1896, pl. xii. fig. 16) does not show the isolated teeth, and is therefore a little unsuited for a detailed comparison. The median, admedian, and outer teeth agree very closely with Hoyle's figure. In the three specimens examined from the Cape, I find the outer teeth do not exhibit such a marked angle between the cusp and the basal portion. This angle is more marked in Jatta's figure, but I suspect this may be the result of difference in orientation. Hoyle shows no cusp on the inner side of the second lateral. This would be a very marked difference, as the cusp is very strongly developed in the Cape forms; but it is indicated in Jatta's figure, so that I am justified in concluding that it is present in the European forms and was overlooked by Hoyle.

I do not consider that there are any differences in the radula between the North and South Atlantic forms large enough to warrant a varietal separation.

*The gladius*.—This structure is figured by Jatta (1896) and Pfeffer (l. c. pl. xxx.), and certain differences are to be noted between these two figures. The Cape specimens are fairly constant in shape, and appear to be midway between the above-mentioned accounts. The "spoon" is smoothly leaf-shaped, as in Jatta's figure; but the extremity is pointed, as in Pfeffer's figure.

#### *Summary.*

A careful consideration of the critical features described above leaves one with a strong impression that the Cape forms are not only specifically identical with the Northern, but also that they do not even constitute a distinct variety. The arms, tentacles, suckers, gladius, and radula offer no constant difference; while such differences as are to be noted, *e. g.* in fin-proportion and denticulation of the suckers, are not sufficiently correlated in the same individuals to lead one to think that they were permanent genetic features. With regard to one of these characters (denticulation of the suckers), we do not possess very full information as to the range of variability in the Northern forms; while the average differences noted above are not large enough in themselves to suggest a varietal difference.

### FAMILY CHIROTEUTHIDÆ.

#### MASTIGOTEUTHIS sp. A.

One specimen (? sex) from Station 277; 820 fathoms.

The specimen is in a very poor condition. The epidermis has been scraped from practically the whole of the body; the visceral sac and head are very badly damaged, and some of the arms are imperfect. A portion of one tentacle was preserved.

The *mantle* is slender and, when intact, was probably shaped like that of *M. flammea* (Chun, 1910). It terminates in a slender prolongation of the gladius. The visceral sac terminates at about 9 mm. from the anterior end of the fin. It is not apparent in the present condition whether the gladius was covered as in *flammea* by quite an extensive pallial continuation, or whether it was practically naked as in *M. grimaldii* (Fischer & Joubin, 1906, pl. xxv. fig. 6). In any case, the termination of the visceral sac is not abrupt as in *grimaldii*, nor yet so near the anterior border of the fin. The mantle and head were apparently covered with numerous light-organs, as a small patch of skin was found on each covered with these structures.

The *fins* seem to be intermediate in shape between *M. flammea* and *M. grimaldii*. Each fin is roughly triangular as in the former, but its anterior and posterior sides are more curved, giving a circular appearance to the pair as a whole. In *grimaldii*

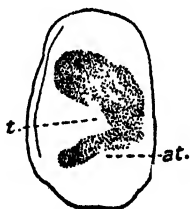
the fins are more or less pentagonal in Joubin's figure (1895, pl. iii. fig. 1), while in the later figure (Fischer & Joubin, 1906, pl. xxv. fig. 6) the sides are asymmetrical. The truth is that lesions and contraction may modify the fin-shape very much, while, in addition, age and other circumstances must unite to render them a very unsatisfactory taxonomic guide.

The relation between the fin-length and the mantle-length has been used by Pfeffer (*l. c.* p. 612), together with the size and direction of the eyes, to separate *flammea* and *grimaldii*. I am very sceptical as to the value of the figures given (fin-length three-fifths of the mantle-length in *grimaldii*, two-thirds in *flammea*). This difference is too slight to be of much value. Thus in our case the ratio is 25 : 41, or actually three-fifths. It is scarcely likely that an additional 2 mm. in the length of the fin necessary to raise it to two-thirds of the mantle could be significant!

The eyes are in very bad condition. The right-hand one has been torn from its socket. The left-hand one is not directed forwards as in *grimaldii* (Joubin & Fischer, 1906); but I do not regard this as of very great importance, as in the same species the eyes are shown (Joubin, 1895, pl. iii. fig. 1) directed more or less laterally.

The articulatory cartilages (text-fig. 13) are very unlike any other known species, owing both to the reduction in size of the aperture

Text-figure 13.



*Mastigoteuthis* sp.  $\times 8$ .

Adhesive organ (left). at., antitragus; t., tragus.

and to the peculiar development of the lobes. In the first of these it is exceeded by *M. cordiformis* Chun; but it is distinguished from that species by the very prominent tragus. The development of the lobes found in this form are foreshadowed in *flammea* (Chun, 1910, pl. xxxv. fig. 3), but in that form the antitragus is very marked, and in any case there is great variation in that species (*cf. l. c.* fig. 4). The form found in *Chiroteuthis* is more comparable to this than the other species of the genus.

*The suckers.*—Certain differences from the allied species, probably of taxonomic importance, are found in the teeth of the sessile and tentacular arms. In the former the teeth of our specimen are far more prominent than in *flammea*. They are

about as numerous as those of *grimaldii*, but not so long. Those of the tentacular suckers differ from those of *flammea* in being very numerous, very closely crowded, and rather short.

Length of tentacle.....	160 mm.
Length of arms: 1 .....	17±1 mm.
2 .....	26±2 "
3 .....	23±2 "
4 .....	65 mm. (L.).

I do not consider that the arm formula is any guide to taxonomic position; but the very considerable size of the tentacle and of the fourth arm, which are respectively four and one and a half times as long as the mantle, are outstanding features. The second of these differentiates this form from *flammea* and *grimaldii*. The only form which approaches the tentacle-mantle ratio is *M. agassizi* (Verrill), while in all the other species the fourth arm is never more than slightly larger than the mantle in length, except in the young specimen of *M. grimaldii* (Joubin), in which it is nearly the same as in this form. The adult of *grimaldii*, however, shows a different size ratio (41 : 41).

On the available evidence I do not consider it safe to regard this form as a distinct species. In several features it seems to be intermediate between *grimaldii* and *flammea*, in others to stand apart from the other known species.

Some ten species of this interesting genus are known, as well as two uncertain forms. Of these, seven and an undetermined fragment comes from the North and Central Atlantic, one (*cordiformis*) is found off Sumatra (Chun, 1910) and the N.W. Pacific (Sasaki, 1920), one is found on the East African Coast in equatorial waters, and two (*dentata* Hoyle and (?) *famelica* Berry) were obtained from the Pacific Ocean. The metropolis of the genus therefore seems to be the North Atlantic, while the affinities of this form are, as we have said, distinctly with the North and equatorial Atlantic forms *grimaldii* and *flammea*. The members of the genus are usually obtained from great depths, nearly all the records being from over 1000 metres, and three coming from over 3000 metres. The development of large rhombic parallel plates recorded by Chun for *M. hjorti* (Chun, 1914, p. 8) is very interesting. The plates in question may be analogous to the epidermal plates of *Moroteuthis*, which are considered by Lönnberg to have a hydrostatic function (*v. above*, p. 598).

### Family CRANCHIIDÆ.

#### Subfamily CRANCHINÆ.

##### PYRGOPSIS PACIFICA (Issel).

One specimen (? ♀) from Station 258, Natal; 100 fathoms.

This specimen, a welcome addition to our limited material of this remarkable genus, is in very good condition. It was

thought inadvisable to dissect a single example of this delicate form, although we are in need of anatomical knowledge of the genus.

Chun (1910, p. 354) regards *schneehageni*, *rhynchophora*, and *zygæna* as synonyms of *pacifica*. Pfeffer (*l. c.* p. 657) separates all four, and gives a somewhat unsatisfactory key to their diagnosis. Until more material is forthcoming, I do not think discussion on the subject is very profitable. In any case, the characters upon which Pfeffer has chosen to discriminate the species are of dubious value. They are considered by him to show specific differences in the fins, supporting membranes of the arms, and in the eye-peduncles. With regard to the fins, I usually find it necessary to treat such evidence with caution. As we have already seen (p. 615), their shape varies with age and they are subject to lesions. From the present example the specimens of *pacifica* described by Issel and Chun differ somewhat in this respect. Though more quadrate in shape and more transversely elongate, the fins of this specimen approach the circular shape of *pacifica* rather than the triangular form of *schneehageni*. In this they agree with the two specimens obtained by the 'Terra Nova' and described by Massy (1916, p. 168).

With regard to the "Schutzsäume," it is again very difficult to draw a line. Issel's figure (*l. c.* fig. 38) shows them well developed, especially on the fourth arm. Chun's figure (*l. c.* pl. lii. fig. 3) illustrates them in the reversed position, but they do not appear to be so wide. They are moderately developed in the present case. Again, as to the ocular peduncles, we here actually encounter an error on Pfeffer's part. He describes the peduncles of *schneehageni* as "geschwollen" and those of *pacifica* as "schlank." Actually his figure (*l. c.* pl. xlvii. fig. 18) shows a very narrow stalk carrying a more distal swelling. The peduncle of *pacifica* cannot very well be described as "schlank" (*cp.* Issel, *l. c.*), as they are stout. Fortunately we can rectify this discrepancy by reference to the 'Terra Nova' material. The specimen from Station 126 has an ocular peduncle exactly like that of Pfeffer's *schneehageni*, while that from Station 139 resembles the type-figure of Issel's *pacifica*. I am strongly of the opinion that the only difference is one of shrinkage.

On the characters actually given by Pfeffer, I do not consider that we have any reason for maintaining any specific difference between *pacifica* and *schneehageni*. There seems to be some marked variation in the proportion of the head. Issel's figure makes the ocular peduncles more than twice as wide as the former, whereas in Chun's figure they are nearly the same width. The South African form resembles Issel's figure in this respect, as does the 'Terra Nova' specimen from Station 139. The shape of the head is also different in the case of Chun and Issel's figures.

There is some marked and important difference in the extent

and tuberculation of the cartilaginous bands. The following list summarizes these:—

	Length of bands.			Number of tubercles.
Issel .....	$\frac{1}{2}$	length of the mantle.		5 + 1
Chun .....	$\frac{1}{4}$	"	"	10
Massy .....	$\frac{1}{2}$	"	" (tubercles).	13 & 16
Cape form	$\frac{1}{4}$	"	"	13 & 16

In the last-named the actual bands only occupied a quarter of the mantle-length, but the tubercles are continued much further up the mantle. This circumstance may serve to explain the marked discrepancy in the above differences. Issel figures a median cartilaginous (?) row which is absent in the other forms.

I would hesitate before reducing *schneehageni* to a synonym of *pacifica*. The arrangement of the tubercles of the cartilaginous bands in *schneehageni* seems to indicate some degree of separation, though it must be confessed that there is otherwise not much difference. The chromatophores correspond in general very closely with Issel's figure.

The shape of the mantle itself is subject to a marked variation. In Issel's figure and in the 'Terra Nova' specimens it is very slender apically, the width diminishing upwards from just behind the mantle-opening. In Chun's figure and in the South African form it is more swollen and cigar-shaped, and the maximum width occurs at about half-way up the mantle.

Another source of variation is in the teeth of the tentacular suckers. Issel's specimen had these suckers wholly toothed, Chun's figure (fig. 2) shows them quite bare, while Massy described the 'Terra Nova' specimens as having the large suckers partly toothed (*l. c.* p. 169). The suckers of the Cape specimens are completely denticulate and, in addition, bear a row of laminae.

On the whole I consider this form to be referable to *pacifica*. The nature of the variation described above (even where the data are reliable) is very ambiguous, and in view of the fact that the Natal form combines many characters of Issel's type with those of Chun's specimen, which again can be shown to exhibit features like Issel's form though differing in others, I feel that we are dealing with a polymorphic species rather than assemblage of distinct forms.

#### *Known distribution.*

Tahiti (Issel); Sagami, Japan (Pfeffer); Atlantic, 0° 29' N., 18° 57' W. (Chun, Thiele); New Zealand (Massy); ? Chili (Pfeffer—*schneehageni*); South Africa (G. C. R.). This wide distribution might be increased by including Verany's Mediterranean *zygæna*, Rochebrune's *rhynchophora* (St. Paul), and Berry's N.W. Atlantic *lemur* (Berry, 1920, p. 298). I am, however, in agreement with Pfeffer in keeping the first two separate; while as for the last, it is somewhat difficult to make a complete



comparison from a provisional diagnosis in which some characters of value are not yet discussed. I am inclined, however, to agree with Dr. Berry's judgment in keeping the North-West Atlantic form as a separate species. On this view, the genus is seen as a cosmopolitan one frequenting tropical and sub-tropical waters, with its metropolis probably in the West Pacific. It is composed of a very polymorphic species (*pacifica*), of which local forms or nascent species are seen in *lemur* and *schneehageni* at the opposite extremes of its distributional area, while *zygæna* and *rhynchophora*, on Pfeffer's view, represent a more definite dichotomy of the genus. A renewed investigation might serve, however, to lessen the difference between them and the *pacifica*-stock.

*LIOCRANCHIA REINHARDTI* Steenstrup, var. *a*.

Three examples (2 ♀ adult, 1 ? immature), Station 100, Natal; 220 fathoms.

The three points of difference on which this form tends to diverge from those previously described have been already discussed (Robson, 1924*b*, p. 6), and there is nothing to add to them. It is desirable, however, to point out the distributional relationship of this form to *L. valdiviæ* Chun.

*L. valdiviæ* is recorded from the Indian Ocean (*v. Pfeffer*, 1912) and from the Kii province of Japan (Sasaki, 1920). *L. reinhardti*, on the other hand, has a very extensive range from the North Atlantic and Caribbean Sea to the South Atlantic, China, New Guinea, and is actually recorded from Peru.

*Valdiviæ* is said to differ from *reinhardti* in the absence of tubercles on its gladius. It may be pointed out that *reinhardti* occasionally exhibits this condition.

In the absence of adequate material we obviously cannot discuss the affinities of these forms to any effect. I do not suggest that *valdiviæ* should be identified with *reinhardti*, though it may very well be that it will one day be treated as a variety of that species. What is interesting, however, is the fact that the more localized *L. valdiviæ* is found in the middle of the horizontal distributional area of the more widely-ranging species. In the Indian Ocean, *valdiviæ* and *reinhardti* are found in practically the same areas, viz. just north and south of the Equator. It may be remarked that of the seven records for *valdiviæ* given by Chun (1910) and Sasaki (1920), five are from 2000 metres or over, one from over 1300 m., and one from 500 m. Of the eight records of *reinhardti*, four are from under 1000 m. We may ask ourselves whether this case of a variety or incipient species occurring in the middle of the range of a more widely-distributed *pelagic* species is not explicable by its more or less permanent acquisition of a different vertical distribution. Many more cases would be necessary before we could establish this, but I may point out that the form named by me *Abralia gilchristi* is structurally very near to *A. morisii* Chun, and occurs in the middle of its range. In

this case *gilchristi* was found (two specimens at different stations) only down to 280 fms.; while *morisii* has a recorded range of 2000 m. to 628 m. (1000-319 fathoms).

*LIOCRANCHIA INTERMEDIA* Robson. (Plate I. fig. 5.)

*Liocranchia intermedia* Robson, 1924 b, p. 6.

One example (♂) from Station 174, Natal Coast; 260 fms.

The following details may be added to the description of the external facies of this interesting form:—

1. The fins project some 6 mm. beyond the tip of the gladius.
2. The chromatophores are less plentiful on the posterior surface of the head than on the anterior.
3. The gladius is ornamented with a row of tubercles over the anterior half of its length.
4. The suckers of the second arms increase in size from the adoral end, the maximum size being attained between the fifth and tenth suckers, after which there is a gradual decrease in size.
5. The "Schutzsaum" of the second arm is markedly frilled by the development of strong transverse ribs.
6. The third arm is stated in the preliminary account to have nineteen pairs of suckers. As stated, it is very difficult to make certain of the exact figure; but in this case it is more likely to be seventeen.
7. The fourth right arm is hectocotylized, not, as stated originally, the fourth left arm. In this it agrees with *Pyrgopsis* and *Cranchia* (s.s.), not with *Liocranchia*. The distal half of the arm is hectocotylized; there is a well-developed swimming membrane, while the "Schutzsäume" are practically absent.
8. On the median area of the tentacular hand there are four rows of suckers with specially long stalks on the ventral side. In both tentacles the proximal median suckers are torn away, so that it is doubtful how they are differentiated in size from the carpal suckers. Of the latter there are four rows of smaller suckers diminishing to two rows.
9. There is a well-developed lateral membrane as previously described. This is probably the equivalent of the carina. Both the "Schutzsäume" persist on the manus, that of the ventral side being especially well-developed with well-marked "querbrücken."
10. On the tentacle the median and admedian suckers are completely toothed. This, again, is a character seen in *Pyrgopsis*, not in *Liocranchia*. In *Cranchia* (s.s.) the suckers are completely toothed only in the adult condition.

In default of more information it is impossible to assign this animal to any definite place among the *Egopsida Consuta*. The possession of four (two on each side) cartilaginous bands place it at once in Pfeffer's *Cranchiiform* group. On the other hand, its long thin *Leachia*-like body and large circular fins suggest affinity with that genus.

**CRANCHIA SCABRA Leach.**

One example (probably ♀) from Station 277, Natal Coast; 820 fathoms.

*Dimensions.*—

Mantle-length (ventral edge to tip of fins); 65 mm. ? + 3.

„ width; 45 mm.

„ aperture, diam.; 28 mm.

Fins, length; 11.25 mm.

„ width (total); 18 mm.

Tentacles, length;  $79 \pm 2$  mm.

Arms: 1st pair; 12.5	} from oral membrane.
2nd „ 20	
3rd „ 26	
4th „ 21.5	

In addition to the specimen 82 mm. long described by Chun (1910, p. 329), Pfeffer ascribes one 90 (? 93) mm. to him, but this may be an error.

The following differences from the previous descriptions may be noted :—

A. The mantle-aperture is, relatively to the total mantle-length, much wider than Chun's largest specimen, viz.  $\frac{28}{65}$  instead of  $\frac{26}{82}$ . This feature is not noticed by Pfeffer.

While I do not think much importance is to be attached to the length-breadth index, owing to the liability to distortion, the mantle-aperture is less susceptible to such disturbance and is of taxonomic value.

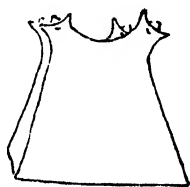
B. Chun and Pfeffer both figure and describe definitely short tentacles which are one-half to two-thirds the length of the mantle. These tentacles have strong bases which seem to taper slightly in the middle and then to expand to form the club. In Pfeffer's variety *tenuitentaculata* they seem to be as long, if not longer than the mantle, and very attenuated in the middle. In the present example they are longer than the mantle and noticeably thinner, if not actually attenuated, in the middle.

C. The cartilaginous tubercles of the mantle (text-fig. 14) have been figured by d'Orbigny (1835, pl. xvii. fig. 5), by Owen (1836, pl. xxi. fig. 5), and by Chun (1910, pl. xlix. fig. 4), but the present specimen exhibits tubercles of a slightly different order.

The first description shows six main divisions of the tubercle, while four is more frequent in the light of subsequent work.

Owen's figure is not very satisfactory. It shows the square shape alluded to below, but the lesser tubercles are not clearly shown, and appear as though they covered the whole of the top. This is, however, not the case in the later descriptions. On the other hand, Chun figures a tubercle which is by no means like that found in the present case. It is true that his figure is based on a half-grown specimen, but the difference in size is not sufficient to lead us to assume that an age-difference in the tubercles is involved. The main differences from Chun's and Pfeffer's descriptions are:—(1) That the main tubercle is not cylindrical in my specimen, but mainly quadrate; (2) the base is larger than the apex in my example. That this is not due to an age-difference can be understood by studying Chun's fig. 4, pl. xlix. The main tubercle would have to be worn down to at least two-thirds of its present size, in order to assume the shape seen in text-fig. 14, in which case the secondary tubercles would vanish altogether; (3) the four secondary tubercles are very much smaller in the Cape specimen.

Text-figure 14.

*Cranchia scabra*. Mantle tubercle.  $\times 16$ .

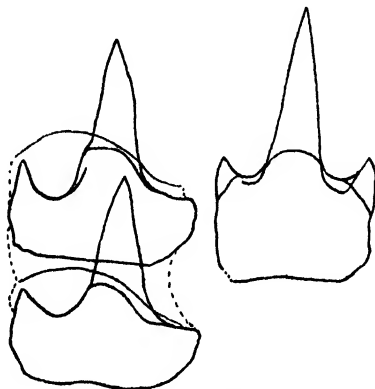
The whole of the mantle is covered by a tough, semitransparent layer of apparently the same cartilaginous nature as the tubercles. The latter are planted on this, but not in close organic continuity with it.

The *mandibles* are rather peculiar. The ventral pair, though in general like those of other Cranchiform (Egopsida), is remarkable for having a small separate plate on each side at the angle between the beak and the anterior ramus. This plate is oblong, tooth-shaped, and appears to be movable on the main structure, to which it is attached by a ligament-like band inserted along the anterior edge of the ramus.

The *radula* (text-figs. 15–16) consists of the usual nine teeth in a row. Of the latter, thirty-six could be counted. The teeth are remarkable for the great size of the last lateral, which is twice the size of the rhachidian. The marginals are large and well-developed. In *Liocranchia gardineri* (1921, p. 434) I was unable to find any marginals, and Massy (1916, p. 169) does not figure any for *Pyrgopsis pacifica*. The ectocone of the first lateral is very strong; no entocone is developed on this tooth, which approximates to the rhachidian in size.

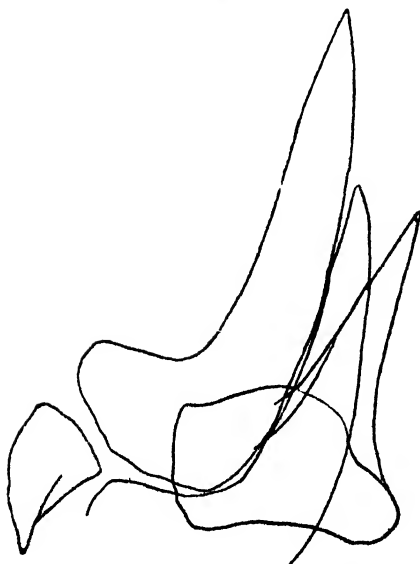
This is a very widely-distributed form, and occurs in the Atlantic, Indian, and Pacific Oceans. It seems to be absent from

Text-figure 15.



*Cranchia scabra*. Radula.  $\times 200$ .

Text-figure 16.



*Cranchia scabra*. Radula.  $\times 200$ .

waters north of  $31^{\circ}$  N. Its southern limit is apparently  $32^{\circ}$  (the present one), though it probably exceeds that in actual fact. It

was not obtained by the 'Terra Nova,' the Deutsche Süd-Polar, or the Scottish National Antarctic Expeditions in antarctic or sub-antarctic waters.

### Sub-family TAONININÆ.

#### GALITEUTHIS ARMATA Joubin.

One example (? ♀) from Station 357 (Cape Town); 900 fathoms.

This interesting form has only been recorded on a few occasions, and the scarcity of specimens warrants the enumeration of certain important varietal data. In the preliminary report (1924b) I followed Pfeffer in regarding *phyllura* Berry, the only other species, as a variety of *armata*. I am now of the opinion that Berry's species is distinct. The following table sets forth certain of the more important diagnostic features in detail, and shows the amount of variation in *armata*.

	1. <i>armata</i> Joubin. (1898.)	2. <i>armata</i> Chun. (1910.)	3. <i>armata</i> Robson.	4. <i>phyllura</i> Berry. (1910.)
<i>Fins</i> (length)	Well over $\frac{1}{2}$ size of mantle.	$\frac{1}{2}$ size of mantle.	Well under $\frac{1}{2}$ size of mantle.	= Mantle.
<i>Fin and gladius</i> (exposed part).	Exceeds total l. of mantle.	$\frac{1}{2}$ mantle- length.	$\frac{1}{2}$ mantle- length.	(No free part of gladius.)
<i>Tentacles</i> :—				
1. Carpal suckers	6 (? 7) suckers and equi- valent knobs.	L. 12 suckers, 5 knobs. R. 5 suckers, 12 knobs.	6 suckers, no pads.	8 suckers, 8 pads.
2. Median suckers (hooks).	13-14	12	10	12
3. Apical suckers ..	12	Four rows of 4 and a few others (? 17 in all).	22-25	16
4. Stalk . . . . .	No suckers shown or described.	Alternating pairs of suckers and knobs.	Alternating suckers.	As in 2.
5. Length .....	About $\frac{1}{2}$ total mantle- and gladius-length.		Just under total mantle- and gladius- length.	Under $\frac{1}{2}$ total length.

The mantle-organ is different in *phyllura* and the Cape form, as the central plate is broader than long and the papillæ are short in the latter, while in *phyllura* the central plate is as long as it is broad and the papillæ are long.

It should be noted in addition to the above differences that in *phyllura* the gladius does not project beyond the fin; while in the Cape *armata* it projects 5 mm. (in a specimen rather shorter than the type), in Chun's specimen it projects some 12 mm. (total length 112 mm.) and in the type it projects still more. This is probably an important systematic difference, though we do not know to what extent shrinkage of the subjacent tissues and damage to the delicate gladius itself may not modify it.

I think the facts given warrant the separation of Berry's *phyllura* from *armata*; while in the present state of our knowledge of this genus I do not think it right to give the Cape form a varietal rank. The absence of carpal pads on the tentacles is very surprising, but Joubin does not refer to them on the stalk of his *armata*, and it is likely that they may fluctuate in their occurrence.

The Cape form shows marked deviation from the Mediterranean form in the shortness of the fins and the combined length of fin and gladius, as well as in the length of the tentacles and the number of the apical suckers. It is, as one would expect, nearer the equatorial form (Chun).

As regards the distribution of these forms, *armata* is known in the adult stage from the Mediterranean, Atlantic, and North Pacific (Sasaki, 1920). Some uncertainty exists as to whether certain larval forms described under different generic names should be attributed to this genus. Whatever may be the truth as to such forms as *Procalistes suhmii*, I do not think there can be much doubt about the Weddel Sea *Galiteuthis suhmii* (Hoyle, 1912, p. 283), though without seeing the actual specimen I would refrain from identifying it with *armata*. *Armata* therefore may be regarded as having a very wide distribution, although one would be grateful for a more complete description of Sasaki's Behring Sea form.

#### ANOMALOCRANCHIA IMPENNIS Robson. (Plate I. fig. 3.)

*Anomalocranchia impennis* Robson, 1924 b, p. 8.

One specimen from Station 540 (Cape Town); 418 fathoms.

A definition of the genus and of the external characters of the species has been already given. It is desirable to add a few comments to the original description of this remarkable form.

I pointed out that, employing Pfeffer's key to the diagnosis of Cranchiform genera, we should place this form among the

*Taonius*-like *Taoniinae*. It should, however, be pointed out now that the apical region of this animal is "spaltachsüßig" according to Pfeffer's terminology (apex of mantle bent ventrally), as in his *Teuthowenia*-like *Taoniinae*. The profile of this form is very like that of *Hensenoteuthis joubini* (Pfeffer, 1912, pl. xlviii. fig. 14). I am, however, a little uncertain whether one can attach much importance to this feature. Against it we must set the projecting gladius and (p. 630 *infra*) the radula, which is far more like that of *Cranchia* (s. s.) and *Desmoteuthis* than *Teuthowenia*. The radula, however, is not a very useful guide at present, as we do not know enough about the radular characters of the *Taoniinae*.

The relationship of this form to the various genera placed in the latter group must remain as originally stated. With regard to the absence of fins, I wish to maintain a reserved attitude. In favour of the likelihood that the animal once had fins is the fact that the thickenings round the end of the gladius originally described are slightly irregular and frayed. In spite of this fraying, the edges are quite even and there is

Text-figure 17.

*Anomalocranchia impennis*. Funnel organ.  $\times 5.5$ .

no trace of special fin musculature. Furthermore, it is inconceivable that any enemy or even disease could have removed the fins on each side so evenly and symmetrically as not to leave a trace. On the whole I believe the animal is finless, but I have exercised a certain amount of caution in using the absence of fins for taxonomic purposes.

For the time being I consider that this animal cannot be accommodated in the scheme provided by Pfeffer's key. It appears to have affinities with the *Taonius*-forms, but to show relationship with the *Teuthowenia*-group on the one hand and the true *Cranchias* on the other.

To the description of the external characters we may add the fact that the sessile arms are all provided with "Schutzsküme."



It may be as well to mention that in the original generic description the edge of the mantle is said to be "flanged inwards." This is a little misleading. Actually the edge is bent outwards and downwards and in some places finally inwards so as to be C-like in section.

The aperture of the funnel, as is usual with the Cranchiida, lacks a valve.

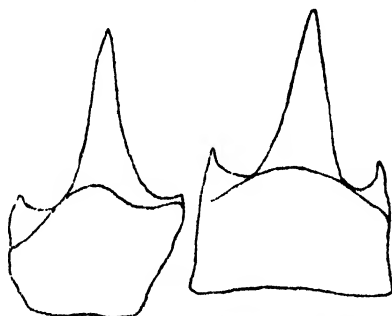
The *funnel organ* (text-fig. 17) is of a form somewhat unusual among the Cranchiidae. The unpaired portion consists of a quadrate median piece and two elongate, ovoid prolongations of the latter which are about as long as the median piece. They bear long and stout papillæ. The paired lateral plates are ovoid and about three-quarters the length of the unpaired portion. The organ is not unlike that of *Galiteuthis* and *Desmoteuthis*, but the limbs of the unpaired piece are much longer and the lateral plates are likewise larger.

#### INTERNAL ANATOMY.

The *mandibles* are rather remarkable for the very small gular lamina of the inferior mandible and the deep palatal lamina of the superior.

The *radula* (text-fig. 18) has markedly tricuspid median teeth, the ectocones of which tend to curve inwards. The admedian

Text-figure 18.



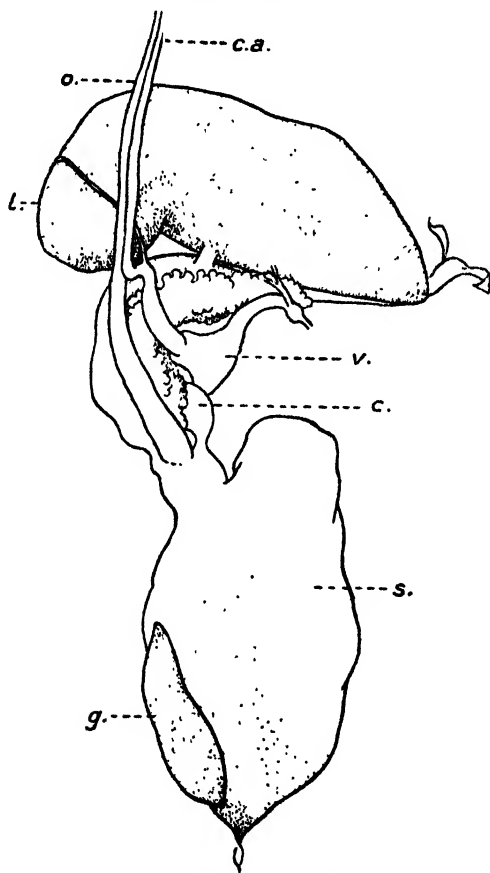
*Anomalocranchia impennis*.  $\times 800$ .

laterals have a low but well-marked ectocone and a feebly-developed entocone situated upon an interiorly-directed process of the tooth. The outer laterals are normal. Very degenerate marginal plates are present. This radula is very unlike that of *Teuthowenia* and *Liocranchia*. The markedly tricuspid rhachidian recalls that of *Desmoteuthis* (Verrill, 1882, pl. xlv. fig. 2 a), while the general plan and the square-based, markedly tricuspid rhachidian teeth are not unlike those of *Cranchia scabra*.

The *oesophagus* (text-fig. 19) runs upwards as a very thin tube for some 35 mm. after quitting the cephalic cartilages. It expands somewhat just before the pylorus. The stomach is irregularly

ovoid in shape. The walls are thin, but in the apical region they are thick and muscular. The œsophageal and intestinal orifices are close together, and are situated in a special muscular diverticulum into which the short bulbous cæcum also opens. This arrangement is very like that in *Desmotenthis* (Chun, 1910,

Text-figure 19.



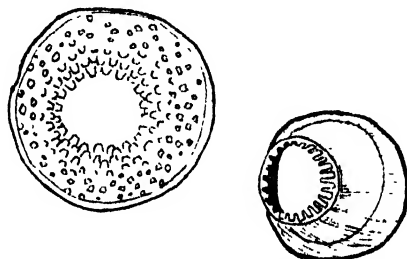
*Anomalocranchia impennis*. Digestive system.  $\times$  about 25.

c., cæcum; c.a., cephalic artery; g., gonad; l., liver; o., œsophagus;  
s., stomach; v., ventricle.

pl. liv.). But in *Anomalocranchia* the cæcum does not project quite so much as in *Desmotenthis*. The proportion and arrangement of the various parts is much more like those in the latter than those in *Cranchia*. The first part of the intestine is thick-

walled and voluminous. It bends over the liver, narrowing down as it does so, and terminates in a narrow rectum. The anus is furnished with two very large leaf-like appendages. The latter are set at right angles to the anus and are not erect as usual, but curl downwards. In *Cranchia*, *Desmoteuthis*, and *Teuthowenia* long appendages are found, while in *Desmoteuthis* and *Leachia* they are leaf-like.

Text-figure 20.

*Anomalocranchia impennis*. Suckers. Tentacular sucker (dentate).  $\times 260$ .

The pancreatic duct opens as in *Desmoteuthis*. The liver, on the other hand, is remarkable, in that it is not spindle-shaped as in the latter and other *Cranchias*, but blunt and bent on itself at the ventral end. It is of a dark red colour, and is covered by the usual lustrous epidermis, which is of a bluish-purple colour in places.

#### *Circulatory System.*

The heart has the same irregular shape seen in *Desmoteuthis*. The point of departure of the anterior aorta is marked by a very definite constriction, and the aorta itself is very short and soon divides into hepatic and cephalic arteries, of which the latter accompanies the œsophagus and divides into two just before the head cartilages. The right efferent artery alone was followed. It leaves its auricle after a very marked constriction. Half-way along its course to the gill is found an expansion of unknown nature, from which is given off a large vessel. There is a well-developed globular branchial heart with an "appendage."

### Tribe 2. **Myopsida.**

#### Family SEPIOLIDÆ.

**HETEROTEUTHIS HAWAIIENSIS** Berry, var. **DAGAMENSIS** Robson.

*H. hawaiiensis* var. *dagamensis* Robson, 1924*b*, p. 11.

Two examples (♀) from Station 176 (Natal Coast) and 251 (Cape Town); 350 and 610 fathoms respectively.

No new additions have been made to this interesting genus since Berry described the Pacific species (1912, p. 319), though additional records of *H. dispar* have come to hand which extend its range in the North Atlantic.

After a careful comparison of this form with the three known species I am surprised to find that it is in closest agreement with Berry's Pacific species. With *dispar* (Vérany) occurring in the North Atlantic (Joubin & Fischer, 1906) and *weberi* at Amboina (Joubin, 1902) it is certainly odd that the Cape form should exhibit closer affinity with *hawaiiensis*. The following description and discussion should leave no doubt in the mind that this identification is correct.

*Dimensions.* -

	Station 176.	Station 251.
Apex of mantle to tip of sessile arms;	37±1	48±1
Medio-dorsal length of mantle;	19	21
Medio-ventral " " "	21	23
Maximum width of mantle;	18	18
Width across fins;	29	36
Max. length of fins;	15	17
Length of fin-attachment;	8	12
Width across eyes;	14	15
Length of dorsal arms; { L.	—	12
" " " { R.	—	12
" second " { L.	—	18.5
" " " { R.	—	15
" third " { L.	—	16.5
" " " { R.	—	15
" ventral " { L.	—	17.5
" " " { R.	—	16.5
" tentacles;	—	32

The body is plump and ovoid in shape. It is thus unlike *hawaiiensis*, which is conical in outline. The dorsal surface is pointed apically, while the posterior is rounded, and these two surfaces are separated, as in Berry's species, by a groove. The dorsal surface is less rotund than the ventral, again as in *hawaiiensis*. The shape of the ventral edge of the mantle agrees with that of *hawaiiensis*, except that the ventral shield, which is well-developed, does not project so far forward. In No. 1 it reaches a line drawn transversely through the middle of the eyes, in No. 2 it only attains a point on a level with the posterior quarter of the eye. In *hawaiiensis* it projects far beyond the eyes. The ventral shield is slightly emarginate as in *hawaiiensis*.

The nuchal attachment resembles that of the Pacific species, but the locking-apparatus differs. The ridge on the mantle is sinuous, the sides of the head-cartilage are not parallel, while the edges are fleshy. The two deep grooves figured and described

by Berry are absent from the ventral surface of the head. The eyes are prominent, but the head is not so wide as in *hawaiiensis*. The sessile arms are connected by an irregularly-disposed web. The arrangement of this agrees with that found in *weberi* and *hawaiiensis*, and differs from that observed in *dispar*. All these arms, except the second pair, show a keel. This special feature is found in *hawaiiensis*, but not in *weberi*.

The arrangement of the suckers is as in *hawaiiensis*, but Berry does not allude to a feature which is very noticeable in the Cape form. In the latter the suckers in most cases have very large columnar bases, which are probably derived from the transverse ridges of the "Schutzsäume." This condition is best seen in the first three rows of No. 2 specimen. The horny rings of the suckers are smooth.

The second pair of arms has the characteristic structure seen in *hawaiiensis*.

The tentacles are fairly long. On the inner side they are angular, while the outer side is rounded. As in the Pacific form, they are slightly tapered and the diameter of the club is less than that of its stalk. The club is beset with numerous minute suckers. The orifices of these are surrounded by a double circle of concentric roughly oblong plates, on the outer side of which is a single row of minute denticles. Berry does not describe the tentacular suckers of this species.

In *hawaiiensis* Berry appears to figure, but does not comment upon, a narrow spindle shaped structure placed at the base of the club along the edge. This structure is very plainly seen in the Cape examples. It measures about 2 mm. long, and is distinguished in colour and texture from the neighbouring tissues. It looks superficially like a tightly-folded fin, but close examination shows that this is not its nature.

The dorsal surface of the mantle and head and the "ventral shield" is covered with a dense mass of purplish and black chromatophores. The fins and the apex of the ventral surface are lighter in colour, both surfaces of the fins being entirely free of colour. The ventral surface of the head is colourless, but the funnel is covered with chromatophores as well as the external surface of the arms. Dark chromatophores are also found on the inner surface of most of the arms. Contrary to what occurs in *hawaiiensis*, a number of reddish chromatophores are found on the distal quarter of the tentacles.

A search was made for the vestiges of a gladius, but without success.

This form is distinguished from the parent species in the following characters:—

A. General shape of the mantle and fins and certain other proportions—e. g., the noticeably greater length from the ventral edge of the mantle to the dorsal arms.

B. The lack of exaggeration in the forward extension of the ventral shield.

C. The narrowness of the head.

D. The columnar bases of the suckers.

E. The presence of chromatophores on the tentacles.

From *dispar* Vérany it is distinguished in common with its parent species by (1) the important differentiation of anterior and posterior surfaces, (2) the presence of a ventral shield, (3) the larger fins, and (4) plump ovoid shape.

From *weberi* it is distinguished by (1) the presence of a ventral shield, (2) the obliquely-set fins, (3) the differentiation of anterior and posterior surface of the mantle\*, (4) the absence of a keel on the second arm, (5) the inequality in size of the sessile arms.

ROSSIA ENIGMATICA, sp. n. (Plate I. fig. 4.)

*Semirossia* sp. A, Robson, 1924 b, p. 10.

Two examples: from Stn. 63 (♀), Cape Town, in 220 fathoms; and Stn. 6 (♂), Cape, in 151 fathoms.

When first examined these specimens appeared to be more closely allied to *Semirossia*. The suckers of the sessile arms in one are very much enlarged and abruptly diminished in size, which is a character diagnostic of that genus. On dissecting the animals, however, it was found that the one with large suckers was a male, the other a female. As enlargement of the suckers of the sessile arms in the male of *Rossia* has been noticed by Jatta (1896, p. 137) and by Chun† (1915, pl. lxiii. fig. 1), there seems no ground for withholding this species from *Rossia*, especially as the majority of the other characters points in that direction. We have, however, to note two interesting features. In the first place, in the male the median suckers are enlarged to an enormous size. They are relatively larger than those of the male *R. macrosoma*, and are even larger than those of *Semirossia tenera* ('Terra Nova' specimens). In the second place, it seems that we have in *Semirossia* a very interesting case of a generic distinction (enlargement of suckers of sessile arms) being founded on a character originally present in the older stock as a sex-limited character. It remains to be noted that the marked attenuation of the arms in the male, and the quadrate median plate of the funnel organ, are features which, with more extensive material and greater acquaintance with the modifications of these organs in other Sepiolids, might warrant a new generic distinction.

\* It is possible that this character may be limited to the female. *H. weberi* is known only from a male specimen.

† In Chun's figure the enlarged suckers of the sessile arms of *R. mastigophora* (♂) diminish abruptly.

*Dimensions.*—

Total length (mantle-apex to tip of 1st arms);	74 mm. $\pm 2$	
Dorsal length of mantle;	27 mm. $\pm 1$ (♀ 24.5)	
Maximum width of mantle;	20 $\pm 1$ mm.	
Fins, width;	47 mm. (both).	
length;	25 $\pm 1$ mm.	
	♂.	♀.
Length of 1st arm pair;	{ R. —	18
	{ L. 27	17
„ 2nd „	{ R. ? 41	—
	{ L. 43 ? + 2	23
„ 3rd „	{ R. } 43 $\pm 2$	{ 25
	{ L. }	{ 27
„ 4th „	{ R. 30 ? + 1	{ 25 approx.
	{ L. 35	
„ tentacles;	{ L. 60 mm.	—
	{ R. 51 mm. (contracted ?).	
„ tentacular club (L.);	15 mm.	

The animal is of the usual *Rossia facies*. The mantle in both sexes is rather longer than broad. The eyes are very prominent. In the male they are slightly wider than the mantle. The neck is fairly narrow. A very characteristic feature, lacking in what is probably its nearest ally, *Rossia mastigophora*, is the very pronounced constriction below the eyes due to the narrowness of the brachial coronet. The fins are almost as long as the mantle, to which they are inserted slightly obliquely. The mantle-edge is markedly undulating, the nuchal prominence, which is far more pronounced than in *R. mastigophora*, being more decided in the male.

Very pronounced differences are found between the male and female as regards the arms.

In the male, in spite of the complete development of the spermatophores no hectocotylyzation was found. But nearly all the arms are remarkable in that their extremities are very attenuate and the suckers are widely spaced, either in pairs or alternating.

Very unfortunately the suckers have been extensively removed from the arms, so that a full account is impossible. There are enough present to make the following statements. On the first arm there is a gradual increase in size over the first eight sucker pairs, which again are followed by six pairs of very large suckers, after which there is an abrupt fall in size. On the right-hand arm the 9th pair was the largest.

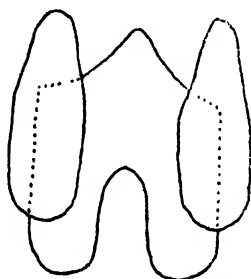
On the second arm the same arrangement occurs except that the increase in size is very rapid, the third and fourth pair being very large.

The third and fourth arms present the same general arrangement of suckers.

The extreme distal suckers are never arranged in more than two rows, and the maximum diameter attained by any sucker is 3.5 mm.

In the female the suckers are almost entirely absent. The arms are of normal size, there being no attenuation of the extremities.

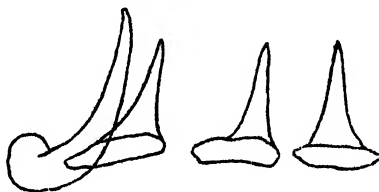
Text-figure 20b.



*Rossia enigmatica*. Funnel organ.  $\times 25$ .

The tentacular stalk is thick and stout over the majority of its length, the club being very gradually attenuated. There is a strong lateral membrane which commences a very short distance before the sucker-bearing region. The suckers of the sessile arms have smooth, very narrow apertures. The aperture measures about a quarter of the total diameter of the chitinous area. The suckers of the tentacles are edentulous, and their outer surface is covered with five or six circlets of plates (more than in *mastigophora*).

Text-figure 21.



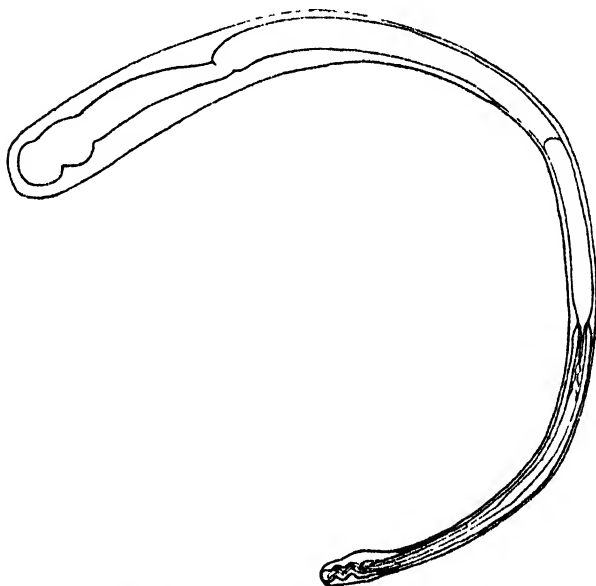
*Rossia enigmatica*. Radula.  $\times 100$ .

The funnel organ (text-fig. 20 b) consists of a quadrate median plate and oblong lateral plates, which tend to become narrower at the ventral end. The main plate is 13 mm. long, the laterals 9 mm. It would be dangerous to generalize as to the structure of this organ in the Sepiolidae, but judging from the figures of *Rossia macrosoma* (Jatta, 1896, pl. xv. fig. 3)



*R. mastigophora* (Chun, 1915, pl. lxiii. fig. 5), and of that of *Semirossia tenera* (B.M. specimens), in all of which the median plate is V-shaped, this form differs essentially from the two genera in question in the quadrate form of this plate. The radula (text-fig. 21) is unlike that of *S. tenera* (Verrill, 1880, pl. xlv. fig. 29) and *R. macrosoma*, in which the bases of the rhachidian teeth are triangular and the cusps of the admedians markedly eccentric. *R. palpebrosa* (Jatta, l. c. fig. 11) shows an approach to the transversely elongate basal plates of this form; but the first lateral is in general of a different shape. Its cusp is markedly eccentric and, owing to the slant of the basal plate, it forms more than a right-angle with the latter.

Text-figure 22.

*Rossia enigmatica*. Spermatophore.  $\times 125$ .

The spermatophores (text-fig. 22) are very unlike those of *Semirossia* (Massy, 1916, fig. 36), and resemble those of *R. macrosoma* (Russell, 1922, fig. 22). There is a difference, however, in that the sac and oral tube are differentiated immediately after leaving the connective, whereas in *R. macrosoma* the oral tube first appears much lower down. The head of the sperin-tube is very much convoluted in this form. This condition is not found in *Rossia*.

It is very interesting to note that the spermatophores are

completely developed, and yet there is no hectocotylization. In *Rossia mastigophora* (Chun, 1915) there is no complete Rossiiform hectocotylization, though the animal has the modified suckers alluded to above. Chun says the animal is not yet sexually mature, though he does not state the grounds for this assertion. To judge by the case of *R. pacifica*, enlargement of suckers in the male does not involve absence of hectocotylization.

This species is generally not unlike *R. mastigophora* Chun; but it differs (*a*) in the form of the funnel organ, (*b*) in the size of the fins, (*c*) in the form of the head and nuchal prominence, (*d*) arm-formula, and (*e*) character of the tentacular suckers. There is, moreover, a very striking difference in the shape of the extremities of the sessile arms in the male and in the diameter of the enlarged suckers of these arms (2.5 mm., Chun; 3.5 mm., Natal specimen). Chun's male example was apparently about the same size as the present one.

A second female from Stn. 46 (260 fathoms) is probably to be attributed to this form. It is larger in size; the mantle is longer relatively to its width, and the outer lateral teeth differ somewhat in the basal plates from *enigmatica*. It is in poor condition, however, and unsatisfactory for description.

#### Family SEPIIDÆ.

ACANTHOSEPION VERMICULATA (Quoy & Gaimard).

*Sepia vermiculata* Quoy & Gaimard, 1833, p. 64.

Two examples (♂): from Stn. 386, 38 fathoms; and ?station ("Natal Coast").

I have no doubt that this form is a representative of the 'Astrolabe' species, although there are two marked discrepancies between the two forms.

The two specimens measure about 6.5 and 6.75 in. in mantle-length, and are therefore smaller than Quoy and Gaimard's example. They each exhibit a fully-modified hectocotylus, so that they are probably mature. The characteristic colour-pattern of *vermiculata* is produced with great clearness, the only difference being that the transverse lines are light on a dark ground instead of the reverse. The lines show the same tendency to fork at one end as in the type.

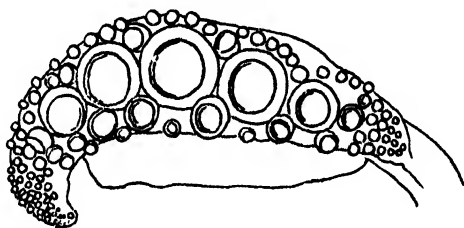
The shell is very like that of the type, except that in the latter the striated area begins to narrow down at a point more than half-way from the rostrum, whereas in this form the reverse is true. The result is that the rostral end of the striated area is more slender in the type.

The shape of the body is different in the two cases, as Quoy and Gaimard figure a very broad form, while the Natal forms

are narrower. I am not, however, inclined to attach much importance to this. A most important difference lies in the tentacular club. Quoy & Gaimard and D'Orbigny figure the latter as having a number of large and small suckers irregularly arranged. They merely say in their respective descriptions that eight or ten are larger than the rest. In the Natal specimen the regular arrangement seen in text-fig. 23 is found. This is very like the condition found in *hierreda* (v. below). Unless the condition figured in the original description is a careless effort to reproduce that seen in the Natal specimen, or is based on a very much disarranged "club," it must constitute a marked difference between the two forms.

Some slight differences are likewise to be noted between the mandibles of the type and our examples. In the lower mandible of the latter the rostral lamellæ do not slant smoothly outwards from the beak, but exhibit a boss or shoulder just below the latter, while the palatal lamella is not ridged as in the type.

Text-figure 23.



*Acanthosepion vermiculata*. Tentacular manus (diagrammatic).  $\times 137.5$ .

The horny rings of the tentacular suckers are not figured, but D'Orbigny says they are "entiers," i. e. not denticulate, which is the condition found in the Natal examples. The rings are provided with narrow necks (interior and exterior) and a large swollen middle portion. The rings of the suckers of the sessile arms are of two sorts. One is perfectly smooth; the other has one-half of its circumference toothed, the other half smooth.

D'Orbigny and E. A. Smith (1917, p. 20) were of the opinion that *hierreda* Rang is possibly identical with this form. There is a good deal to be said for this view, but the following points should be stressed:—

- (1) *Vermiculata* does not show the curious lateral lunulæ of the mantle-surface seen in *hierreda*. While in the latter there is a kind of coarse vermiculate pattern on the smooth surface, it does not take the form of two lateral series of fine forked lines.

- (2) The suckers of the tentacle in Rang's figure (1837, pl. 100) are neither in size nor arrangement like those of *vermiculata*, though in D'Orbigny's figure of *hierreda* they are of that nature.
- (3) The shell of *hierreda* differs slightly in having its posterior sides narrower than in *vermiculata*.
- (4) The horny rings of the tentacle suckers of *hierreda* are like those of *vermiculata*, but those of the sessile arms, when seen in profile, consist of three distinct zones, of which the median far exceeds the inner and outer in *vermiculata*, whereas in *hierreda* the difference is not so excessive.

Bearing in mind the northern range of *hierreda* (Goree, Rang) I am inclined to think that this form may be a northern variety of *vermiculata*, if not a distinct species.

*Vermiculata* differs very markedly from *S. simoniana* (Thiele, 1921) in other respects, though there is a suggestion of resemblance in the shells of the two species.

#### RHOMBOSEPION CAPENSE (d'Orb.).

*Sepia capensis* Férussac & d'Orbigny, 1832, p. 278.

*Sepia australis* Q. & G., Robson, 1924 b; E. A. Smith, 1917, p. 24.

Three examples	(♂)	from Stn. 20;	67 fms.	} Cape Town.
Two	(♀)	..	54; 121	
Three	(♂, ♀ ♀)	..	44; 85	
Young:—				
Twelve examples	(6 ♂, 6 ♀)	..	7; 112	
Ten	(2 ♂, 8 ♀)	..	9; 100	}
Two	(1 ♀, 1 ? ♂)	..	2; 117	

Hoyle and Smith both regarded this species as a synonym of the Australian *australis* Quoy & Gaimard, while Férussac and D'Orbigny themselves were of the same view (though they unjustifiably assumed the priority, cf. Hoyle, 1909, p. 266). *S. "capensis"* has been recorded from Australia by Chapman (1912, p. 24) and Whitelegge (1889, p. 282). Such an identification, if accurate, would of course be very remarkable, for the Sepiidae are littoral animals inhabiting shallow water, and the occurrence of the same species of the genus in Australia and off Cape Town would raise many interesting questions\*. After considering the evidence in the light of the material now available, I am emphatically of the opinion that, as far as the structure of the animals is concerned, the case is "not proven" and is in all probability erroneous.

\* It should be noted, however, that Massy (1918, *passim*) has identified several Bay of Bengal species of *Sepia* with Japanese forms, while, according to her, *Doratosepton kobienensis* ranges from the Persian Gulf to the Pacific.

There are very marked differences between the animals described by D'Orbigny on the one hand and Quoy and Gaimard on the other. They may be summarized as follows:—

- (1) The mantle of *australis* is acuminate and pointed apically.  
The mantle of *capensis* is rounded apically.
- (2) The fins are widely separated apically in *capensis*.  
" " approximated " " *australis*.
- (3) The tentacular "hand" has very large and small suckers regularly arranged in *capensis*.  
The tentacular "hand" has no such disparity in size, and the arrangement is different in *australis*.
- (4) The ratio of width to length is 3 : 5 in *australis*.  
" " " " " " 1 : 2 " *capensis*.
- (5) The "greatest width of the mantle is at the middle in *capensis*.  
The greatest width is at the anterior end in *australis*.
- (6) The shell is shouldered and square apically in *australis*, and it has four ventral furrows.  
In *capensis* the shell is acuminate and pointed, and it has two ventral furrows.

The accounts agree in details of colour, arms, and general shape of the fins, though the data available for comparing the suckers of the sessile arms are very meagre. The specimens obtained by Dr. Gilchrist agree with *australis* in respect of (1) and (2). These, however, may be somewhat heavily discounted, as (*a*) the actual body-shape agrees with *capensis*, and it is only the apex which is like that of *australis*; and (*b*) I do not consider that such a difference as the width between the fins is as important as (3), (5), and (6). However, the likeness is not to be lost sight of.

The Natal specimens agree with *capensis* in (4), (5), and (6), while in (3), though the resemblance is not exact, it is very close, and certainly is highly suggestive of the type of tentacular "hand" figured by D'Orbigny.

On the other hand, they differ from *capensis* D'Orb. in (1) the possession of a deep purple band on either side of the ventral surface; (2) the possession of a membrane on the tentacular manus.

I am inclined to think that (1) is suggested in the description of *australis*, when we read "le ventre est pointue de laque et de brun sur les côtes," but the figure shows a faint general scattering of (*sc.*) pigment spots and not the heavy purple bands seen in the Natal examples.

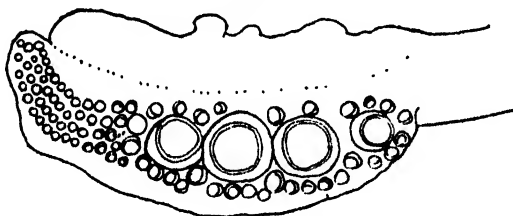
On the whole there is a very marked agreement between D'Orbigny's figure of *capensis* and our Natal specimens and others from the Cape preserved in the British Museum, with regard to the shell; the only difference is that in the Natal examples the last loculus seems to be a little smaller than in the others.

If we were to rely merely on Quoy and Gaimard's figure and description for our knowledge of *australis*, we might very well be misled by a single specimen; but from the figure of the shell obtained on the Victorian coast (Chapman, *l. c.* pl. i.), and from an examination of an undoubted example from New South Wales (British Museum), I cannot have any doubt that the Australian form is very distinct from the South African, although there are certain features in common. The latter, however, I do not regard as of the same importance as the evidence of the shell and tentacle.

The tentacle is figured (text-fig. 24), and it will be seen to agree fairly closely with that figured by Thiele (1920), though the proximal half-sized sucker is missing in the latter. Thiele's figure is not very good, and it is impossible to make out the structure of the distal extremity, but it appears to be less elongate and oblong than ours.

I have discovered no teeth on any sucker rings, whereas a

Text-figure 24.



*Rhombosepion capense*. Tentacle.  $\times 6$ .

semicircular group is found on the sessile arms by Thiele. The rings in this form are likewise smaller than in the Natal form. The shell figured by Thiele agrees very closely with that of the Natal form.

#### *RHOMBOSEPION ACUMINATA* (Smith).

*S. acuminata* Smith, 1917, p. 21.

*Sepia* sp. A (part) Robson, 1924 b.

Two examples ( $\text{♀}$   $\text{♀}$ ) from Stn. 95 (Natal coast); 45 fathoms.

" " ( $\text{♂}$   $\text{♂}$ ) " 103 ( " " ); 160 "

This species was described by E. A. Smith from the shell alone, so that the following notes on the soft parts constitute our first information on the subject.

The shells of the Natal examples resemble Smith's type-specimens very closely, and I can find no significant points of difference. The Natal forms are rather smaller than Smith's largest specimen, but smaller ones were included in those which Smith described, so that a representative series is available for comparison.

*Dimensions.*—

Mantle, total dorsal length;	81 ± 2 mm.
" " " width;	42 ± 1 "
Fins, maximum width;	9 mm.
Width of mantle-aperture;	37 "
" head;	39 "
Length of tentacles;	R. 82 ? + 2; L. ? 90 mm.
" 1st arm pair;	R. and L. 26 ± 1 mm.
" 2nd "	R. 28; L. 30 "
" 3rd "	R. 27; L. 28 "
" 4th "	R. and L. 31 mm.

The animal is of a normal shape externally. The mantle is rather narrow, and terminates apically in a blunt point. The fins are somewhat wider apically, and are separated from each other by a fairly wide space. They project well beyond the apex, but are not continuous as in *S. venusta*. The eyes are moderately prominent. The arms do not call for particular comment. The first two pairs are rounded externally, the last two are keeled, the keel of the ventral pair being very marked and extending upwards over the cephalic integument as far as the level of the funnel.

There are four alternating rows of suckers on the sessile arms, the two median rows of which on the fourth pair are larger than the external rows. The horny rings of the suckers in all cases examined bear minute denticles on half their circumference.

The tentacles are roughly triangular in section. The "hand" has a sucker-bearing area 10·5 mm. in length by 3·5 in width. This is covered by numerous small and closely-set suckers, which bear some 7-9 prominent teeth on the distal side of the periphery. The tip of the manus is recurved, and a rather narrow membrane runs upwards, extending to about 4·5 mm. beyond the manus proper. Between this and the sucker-bearing area is a very strongly-marked fold, extending the whole length of the manus and continued beyond the sucker area for some 2 mm.

The *hectocotylus* is, as usual, on the left ventral arm. The oral and distal thirds are normal. In the median third the ventral edge of the arm is raised somewhat above the dorsal edge, and carries a single row of very small suckers. The fact that in this region these are slightly biserial distally and proximally suggests that this row represents the original two ventral rows. On the dorsal side are two alternating rows of minute suckers, which represent no doubt the two dorsal rows.

The *funnel organ* has a V-shaped median plate. The arms of this are thick (4 mm.) and their sides parallel. At the junction of the arms is a narrow ridge lying in the sagittal plane. The lateral plates are long and very narrow (14 × 3·5 mm.).

There is a well-developed tongue-shaped *funnel valve*. The

*locking apparatus* in both adults agreed in the character of the funnel plates, which have eccentric semilunar depressions which do not extend upwards to the margin.

The colour is a uniform dark brownish purple on the dorsal surface of the mantle, head, and arms; while on the posterior surface of the mantle the deep purple is replaced by a light reddish brown, which is still lighter on the head and arms. The fins are of a faint brownish-red ground-colour, with a scattering of minute dark chromatophores.

*RHOMBOSEPION HIERONIS*, sp. n. (Plate II. figs. 9, 11.)

*Sepia* sp. A, Robson, 1924 b.

One example (♂) from Stn. 8, Cape Town; 126 fathoms.

Two examples (♀ ♀) „ 7\*, „ „ 112 „

One example (?) „ 33, „ „ 150 „

Two examples (?) „ 2, „ „ 117 „

The status of this form has been a considerable source of difficulty. As will be seen, there are substantial differences between it and *acuminata*. Nevertheless the points of agreement are fairly strong. It might seem desirable, without a more extensive series, to stress the resemblances rather than the differences. But I cannot imagine any supplementary data bridging the gap with regard to the characters of the arms and hectocotylus.

*Dimensions.*—

Dorsal length of mantle; 57 mm.

„ width „ 28 „

Fins, max. width; 6.5 mm. (in a specimen 61 mm. long).

Head, „ „ 28±1 mm.

Mantle-aperture; 28±1 „

Length, 1st arm pair; 21 mm. }

2nd „ 23 „ }

3rd „ 26 „ }

4th „ 26 „ }

approximately.

tentacles { R.; 49 mm.

{ L.; 57 „

The general shape is like that of *acuminata*, except that the mantle-aperture is relatively somewhat wider.

The fins are slightly narrower. Owing to their crumpled and distorted condition it is not possible to be certain as to their shape, but in one example at least the increase in width towards the apex is not so marked as in *acuminata*. The arms do not differ from those of *acuminata* very much in their general shape. The arm-formula differs, but not much importance is to be attached to this.

\* Not 108 as originally stated.



Some marked differences occur with regard to the suckers. In the sessile arms of the female there are only two rows on the dorsal arms; while in the male there is (as in *Rossia*, etc.) on the second and third arm pairs a patch of very much enlarged suckers, an uncommon feature in the Sepiidae. There is the same disparity in size between the inner and outer rows of suckers on the normal fourth arms as in *acuminata*. The rings of the suckers of the sessile arms are smooth. The tentacular manus differs slightly from that of *acuminata*. The sucker-bearing area is rather shorter and broader, the suckers are less crowded, and the fold above described in *acuminata* tends to be shorter. The suckers are edentulous, but their wide rings are beset with numerous small knobs. Moreover, the manus itself is usually more recurved than in *acuminata*. The hectocotylus is very characteristic, and is far more modified than in *acuminata*. The arm exhibits three main areas:—(a) a distal series of minute paired suckers; (b) a median area of enlarged toothed suckers similarly paired; and (c) a proximal area in which the arm is conspicuously flattened laterally and deepened, and bears a single ventral row of minute suckers which occupies the actual oral surface and two dorsal rows of alternating and equally minute suckers. The adoral patch of unmodified suckers found in *acuminata* is absent, but a single large sucker is found in this position. The character of the hectocotylus recalls that of *acuminata*; but the type is far more exaggerated than in that form, the great depth of the arm itself in *hieronis* rendering it at once distinguishable.

The shell in general is very like that of *acuminata*, and for a long time I was under the impression that they were identical. There is, however, one constant difference. The striated area and last locus are more elevated and slope away rather abruptly at the sides, giving rise to two narrow lateral areas, in which there is a marked sinuosity of the striae. In young examples these areas are traversed by a well-marked groove. This condition seems to be indicated in Smith's figure of *acuminata* (l.c. pl. xi. fig. 3). But an examination of his specimen shows that this is not the case.

The funnel organ has a more massive central plate than *acuminata*. The apex of the V tends to be more drawn out and the extremities to be more expanded than in that form, though these are by no means constant characters. The funnel valve is likewise not so tongue-like as in *acuminata*, its sides being bent downwards to form a more triangular profile.

The funnel plates of the locking apparatus show constant differences from those of *acuminata*, their concavity being central, wider, and not so long, corresponding to shorter and broader studs on the mantle side.

It will be thus seen that there can be no doubt as to the specific distinction of *hieronis*. It has close affinity with *acuminata* in the character of its external parts and shell; but the

nature of its hectocotylus, the suckers of sessile arms and tentacles, the locking apparatus, and, in a lesser degree, of the tentacle and funnel organ render it very distinct.

I am unable to find any species that approximates to these two forms. *S. lefebvrei* D'Orb. (Hoyle, 1907, p. 39) is not unlike *hieronis* in general shape, but it differs substantially in many details. As Smith says (*l. c.* p. 21), Pfeffer's *venusta* (preocc.) comes near to *acuminata*. As the former is a Zanzibar species, the suggestion is not implausible; but *venusta* is in all probability a young form, and the figure given by Pfeffer (1884, fig. 15) shows that the fins at least are very different in shape etc. from either *acuminata* or *hieronis*. I am of opinion that *hieronis* is a derivative of *acuminata*. It should be noted that Smith records the latter from Port Elizabeth.

#### DORATOSEPION CONFUSUM (Smith).

*Sepia confusa* E. A. Smith, 1917, *l. c.* p. 24.

One specimen (♂)	from Stn. 107,	Natal Coast;	180 fathoms.
Two specimens (♂)	.. 95,	.. ..	192 ..
Two .. (♀)	.. 102,	.. ..	158 ..
One specimen (♀)	.. 167,	.. ..	36 ..

As this form is the subject of a memoir (now in the press) by Miss A. L. Massy, I refrain from any detailed discussion of its structure. The remarkable sexual dimorphism manifest in the possession of "tails" by the males of this species has already been described (Massy and Robson, 1923). A more detailed examination of the histology of the "lateral organ" on the extremity of the "tail" is in progress.

A curious feature that was not noticed in the original publication is that the dimorphism is extended to the sessile arms. As was originally stated, the fourth arm of the male is not hectocotylized, and the sessile arms show in most cases four rows of suckers that extend down to their tips. This is clearly seen in all cases (save in one or two arms that are damaged). In the female, however, the arms are normal up to the distal quarter, where they become attenuated; the suckers usually become biserial, and the "Schutzsäume" become very much folded inwards. In the male the arms become likewise attenuated. Occasionally the suckers seem to be reduced to two rows, but, unlike the condition in the female, the occurrence of two rows is very uncommon. This circumstance originally prompted me to suppose that two different species were involved. A long and careful examination of the shell, the other features of the sessile arms (including the suckers), the tentacles, the fins and other external features, the locking apparatus and funnel organ gave, however, no trace of specific distinction. The suckers, shell, tentacles, locking apparatus, radula, and mandibles in particular are identical in both cases. A certain amount of

divergence with regard to the funnel organ is found, but it shows no correlation with the dimorphism of the fins and sessile arms.

This species shows marked affinities, as far as concerns the only common structure known (the shell), with *D. burnupi* and *insignis*, both from Natal. It is uncertain, however, what the latter species are, as they are known only from a limited number of shells. The genus is recorded from the Red Sea, Indian and Pacific Oceans.

*SEPIELLA CYANEA* Robson. (Plate II. fig. 6.)

*S. cyanea* Robson, 1924 *b*, p. 13.

One specimen (♂) from Stn. 476, Natal Coast; 28 fathoms.

One " (♀) " 389, " " 60 "

In the introduction to the original description of this form it was stated that it was impossible to find any form that approximated to it. The details on which it was there stated to differ from the known species were not very fully given, and may be amplified here.

The visceral sac is elongate and thimble-shaped, the dimensions being approximately  $33 \times 79$  mm. The proportions of the mantle are alike in male and female, and are unlike those of *inermis* Stp., recalling those of *maindroni* Rochebr. The original description of "cone-shaped" does not do justice to the fact that the sides are scarcely divergent and the apex very broad and blunt.

The fins are narrow in front and widen rapidly posteriorly, measuring some 10–11 mm. at their widest. They are closely approximated, and in fact tend to overlap at their dorsal extremity, though they are separated by a deep notch as in *inermis* (Massy, 1916, p. 231). They are unlike those of *S. maindroni*. At the apex of the mantle is found the ventral pore characteristic of the genus.

The arm-formula is 4. 3. 2. 1, though the first three pairs may be subequal. All the arms are keeled, the keel of the fourth being the strongest. In *maindroni* the carination is very obscure. As in Massy's described specimens of *S. inermis*, the suckers of the sessile arms in the female are smooth, though they occasionally show a certain amount of notches. The suckers of the male, though they agree with *inermis* in general plan, differ in detail. The proximal suckers are almost smooth: the median ones have some twenty teeth and the distal ones fifteen. These are far more numerous than in *inermis*.

The form of the tentacular manus agrees very well with that of *inermis*, even to the possession of the two enlarged suckers at the extremity. They differ, however, in the number of teeth on the suckers, which are less in *cyanea*, a male of 84 mm. having only eight teeth on an average. The hectocotylus (text-fig. 25)

differs from that figured by Hoyle (1905, p. 982) for *inermis*. The extremity of the arm is very long and attenuated instead of short and broad. In the modified area the same general pattern is visible as in *inermis*, but there are differences in (1) the number of rows of suckers, (2) the position of the suckers, and (3) the arrangement of the transverse ridges.

The cephalic plates of the locking apparatus (text-fig. 26) are not unlike those of *inermis* (Steenstrup, 1880, fig. 5, p. 352), but the external border is parallel to the sides of the depression and not produced into a lobe as in *inermis*.

The shell of *cyanea* tends to differ somewhat from that of *inermis*. Both the examples obtained are very narrow, their length-breadth index being 32 and 29, whereas the lowest found in *inermis* is 37. The striated area is narrower and more pointed

Text-figure 25.



*Sepiella cyanea*. Hectocotylus. Natural size.

in the male than in the female. The knob on the dorsal surface described in the original report is probably not of taxonomic value. It is absent in the female, and has the appearance of a repair-outgrowth.

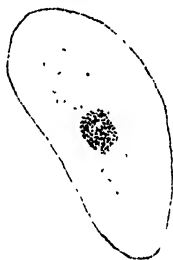
The radula of *inermis* has been figured by Massy (*l. c.* pl. xxiv. fig. 11, not xxiii. fig. 6). A comparison between this and text-fig. 27 shows certain well-marked and constant differences in the teeth.

The ground-colour is a deep purplish blue on the anterior surface, which changes to a dull mauve on the posterior. On the former the edges of the fins are light, and a series of elongate wedge-shaped patches of red colour are disposed transversely with the bases of the wedges on the fins. These ocelli are found only

in the male, as in *inermis*; but in the latter they are round or pear-shaped (Massy, *l. c.* p. 235).

The affinity of this species obviously lies with *inermis* and *maindroni*. The former has a wide range of distribution from the Persian Gulf to Japan (Joubin?). The latter is recorded from Pondicherry and Japan (Rochebrune, 1884, p. 89; Hoyle, 1886, p. 148). For the time being it is very difficult to decide as to the relationship of these forms. The bulk of the general resemblance

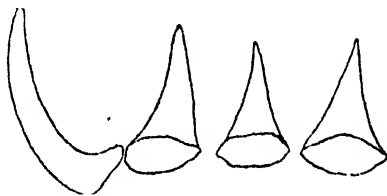
Text-figure 26.



*Sepiella cyanea*. Adhesive organ.  $\times 3$ .

certainly lies with *inermis*, from which it is obviously distinct specifically (1) in general shape, (2) colour-pattern of male, (3) radula, (4) hectocotylus, and (5) certain details of the dentition of the suckers. It is very unfortunate that there is only one complete specimen of *maindroni* available for study. The tentacular manus of this is in very bad condition and useless, and the general condition is poor. The shape of the mantle, the funnel organ, the suckers of the sessile arms, and the shell, all tend

Text-figure 27.



*Sepiella cyanea*. Radula.  $\times 35$ .

to resemble *cyanea*, but the tentacular suckers, fins, size, carination of arms, and arm-formula all differ. I am inclined, therefore, to think that *cyanea*, while distinct from both *inermis* and *maindroni*, has affinities with both, though those with *inermis* are closer. It is worth while noting that *maindroni* (1 specimen, 1-50 fathoms) and *cyanea* (2 specimens, 28 & 40 fathoms) are, as far as the very scanty evidence goes, only known from shallow water, while *inermis* (Massy, *l. c.* pp. 232-233) is found down to 400 fathoms.

## Family LOLIGINIDÆ.

## LOLIGO.

The two large forms recorded below are given temporary designations, as they are both represented only by a single adult specimen, and their relationships with other forms are such that a large series is necessary to arrive at a satisfactory conclusion.

## LOLIGO A.

*Loligo* A (part) Robson, 1924 b.

One example (♂) from Station 88, Cape Town; 33 fathoms.

*Dimensions.*—

Length of mantle (dorsal);	133 mm.	
Width of mantle;	29	"
Length of fins;	76	"
" " (total);	74	"
Width of mantle-aperture;	27	"
Length of 1st arm;	44	"
" 2nd "	55	"
" 3rd "	61	"
" 4th "	48	"
" tentacles;	? 112	"

}  $\pm 2$  (R.).

The mantle is long and fairly slender, the sides being more or less parallel for about half the length. The fins are rather more than half the body in length, and their anterior margin is slightly less than the posterior in length. The nuchal prominence is short.

The sessile arms have the median suckers of the second and third pair (only) very much larger than the adoral and distal suckers. The suckers have 9-10 denticles placed as in *indica* Pfr. and equalling those found in that species in number (cf. Goodrich, 1896, p. 7). The denticles are not unlike those of *L. indica* in shape, but they are more irregular, and some on each sucker are much wider than the rest.

In the tentacles the external rows of suckers are slightly less in diameter than the median rows, but the latter are not very much enlarged (e.g. as they are in *reynauldii* D'Orb.). The denticulation of these suckers seems to be intermediate between those of *indica* (Goodrich, l. c.) and those figured for another form (probably attributed in error to *indica*) by Hoyle. The teeth number 20 on an average, and are not nearly so widely spaced as in *indica*. A certain disparity between the median and lateral suckers was

observed, the latter having longer teeth and being rather less in number. The hectocotylized arm shows 14 pairs of normal suckers, then a modified pair, that on the ventral side having a long stalk and that on the dorsal being very small. These follow the usual papillæ, which have broad bases on the ventral side and are slender on the dorsal. The dorsal "Schutzsaum" is very much thickened and enlarged in the area parallel to the first seven pairs of suckers.

There are some 3 to 5 suckers on each of the labial pillars. These exhibit some seven squarish denticles.

This form seems to have most in common with *indica*, from which it is, however, probably specifically distinct.

It possibly has some community with the group formed by *plei*, *spectrum*, and *bleekeri*.

It differs from *reynauldii*, the commonly recorded Cape

Text-figure 28.



*Loligo A.* Radula.  $\times 35$ .

species, in (1) the tentacular and sessile arm suckers, (2) the proportion of the fins, (3) the absence of very much enlarged suckers on the tentacle, (4) the small size of the nuchal prominence, (5) the absence of the median dorsal colour-band, and (6) in certain features of the radula. The colour (in formalin) is more or less flesh-tinted, with fairly densely and evenly distributed and reddish-black chromatophores. These become larger between the eyes in the dorsal region, and are somewhat denser on the dorsal surface of the mantle.

The *radula* (text-fig. 28) seems to agree on the whole with that of *reynauldii*, but (1) the marginals are far more curved; (2) the second lateral has an inner heel, which is absent in *reynauldii*; (3) there is less disparity in size between the main and lateral cones of the rhachidian and adlateral teeth. From what can be made out of the figure of *indica* (? Massy, l. c. pl. xxiii. fig. 6), that species has certain features in common with *reynauldii* and the present form.

**Loligo B.***Loligo A* (part) Robson, 1924 *b*.

One example (♂) from Stn. 188, Natal Coast; 33 fathoms.

" " " " unknown Station.

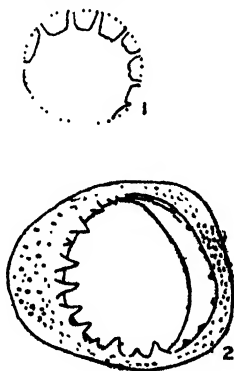
This form upon more detailed observation proves different in so many respects from the preceding form that it must be provisionally regarded as specifically different. It should be noted that both the forms are represented by males.

*Dimensions.*—

Dorsal mantle-length;	208 mm.
" " width;	43 "
Width of fins (total);	110 "
Length of fins;	130 "
Mantle-aperture;	41 "
Length of 1st arm;	51 "
" 2nd "	66 "
" 3rd "	75 "
" 4th "	65 "
Tentacles (R.) (approx.);	143 "

The mantle is more slender than that of the preceding form, the apical region being markedly narrow. The fins, if anything, are somewhat longer in proportion to the mantle. As in form A, the posterior margin exceeds the anterior in length.

Text-figure 29.

Sucker teeth of (1) *Loligo A*; (2) *Loligo B*. (Sessile arms.)

The suckers (text-fig. 29, 2) of the sessile arms do not show the same disparity in size of the various arm pairs as noted above. These suckers show some nine completely-developed denticles which more or less agree with *spectrum* (cf. Massy, 1916, p. 221).



observed, the latter having longer teeth and being rather less in number. The hectocotylized arm shows 14 pairs of normal suckers, then a modified pair, that on the ventral side having a long stalk and that on the dorsal being very small. These follow the usual papillæ, which have broad bases on the ventral side and are slender on the dorsal. The dorsal "Schutzsaum" is very much thickened and enlarged in the area parallel to the first seven pairs of suckers.

There are some 3 to 5 suckers on each of the labial pillars. These exhibit some seven squarish denticles.

This form seems to have most in common with *indica*, from which it is, however, probably specifically distinct.

It possibly has some community with the group formed by *plei*, *spectrum*, and *bleekeri*.

It differs from *reynauldii*, the commonly recorded Cape

Text-figure 28.



*Loligo A.* Radula.  $\times 35$ .

species, in (1) the tentacular and sessile arm suckers, (2) the proportion of the fins, (3) the absence of very much enlarged suckers on the tentacle, (4) the small size of the nuchal prominence, (5) the absence of the median dorsal colour-band, and (6) in certain features of the radula. The colour (in formalin) is more or less flesh-tinted, with fairly densely and evenly distributed and reddish-black chromatophores. These become larger between the eyes in the dorsal region, and are somewhat denser on the dorsal surface of the mantle.

The *radula* (text-fig. 28) seems to agree on the whole with that of *reynauldii*, but (1) the marginals are far more curved; (2) the second lateral has an inner heel, which is absent in *reynauldii*; (3) there is less disparity in size between the main and lateral cones of the rhachidian and adlateral teeth. From what can be made out of the figure of *indica* (? Massy, l. c. pl. xxiii. fig. 6), that species has certain features in common with *reynauldii* and the present form.

## LOLIGO B.

*Loligo* A (part) Robson, 1924 b.

One example (♂) from Stn. 188, Natal Coast; 33 fathoms.

" " " " unknown Station.

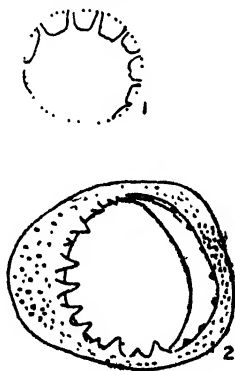
This form upon more detailed observation proves different in so many respects from the preceding form that it must be provisionally regarded as specifically different. It should be noted that both the forms are represented by males.

*Dimensions.*—

Dorsal mantle-length;	208 mm.
" " width;	43 "
Width of fins (total);	110 "
Length of fins;	130 "
Mantle-aperture;	41 "
Length of 1st arm;	51 "
" 2nd "	66 "
" 3rd "	75 "
" 4th "	65 "
Tentacles (R.) (approx.);	143 "

The mantle is more slender than that of the preceding form, the apical region being markedly narrow. The fins, if anything, are somewhat longer in proportion to the mantle. As in form A, the posterior margin exceeds the anterior in length.

Text-figure 29.

Sucker teeth of (1) *Loligo* A; (2) *Loligo* B. (Sessile arms.)

The suckers (text-fig. 29, 2) of the sessile arms do not show the same disparity in size of the various arm pairs as noted above. These suckers show some nine completely-developed denticles which more or less agree with *spectrum* (cf. Massy, 1916, p. 221).

But there are usually about three additional ill-developed denticles, not noticed in *spectrum*, and, in addition, at the adoral side of the circumference of the sucker some nine minute rudimentary denticles can always be seen.

The normal teeth are short, acute, and triangular in shape. There is no differentiation between the median and other suckers in respect to their dentition as in *spectrum*. The tentacular suckers are remarkably uniform in size. The latter decreases very abruptly at the distal quarter, but otherwise they vary but slightly from row to row. They are each provided with some 23-24 teeth, which are shorter and more stumpy than those of *Loligo* A and far less numerous than in *spectrum*.

The oral pillars bear some 5-7 suckers. These bear more denticles than in the preceding species, viz. 10-11. The hectocotylus bears some 19 pairs of unmodified suckers (exclusive of the initial one); these are succeeded by a pair modified as in *Loligo* A. The papillæ which follow next are different from those of *Loligo* A in that the broad bases found in A on the ventral papillæ are not found in this case, the two rows of papillæ, though differing in size, being far more alike in shape. The dorsal "Schutzsaum" is not modified as in A.

The colouring resembles that of the preceding, except that the chromatophores are not so much concentrated on the dorsal surface of the mantle, while they seem more dense towards the edge of the fins.

The suckers of the tentacles and sessile arms, the relation of the length of the fins to the mantle-length, the colour and the character of the tentacular manus differentiate this form from *reynauldii*, though there are noticeable resemblances in the radula. But it is difficult to suggest with which form its affinity lies. Its build seems to foreshadow the widely-spread Indo-Pacific *spectrum*, but there are some noticeable differences in regard to the denticulation.

Taking these two forms together, one would say that on the whole their affinity lies with the Indian Ocean forms, but that both show a certain amount of relationship with the W. Coast *reynauldii*. This suggests that the *Loligos* are not so much affected by hydrographical separation as other forms.

To judge by the previous reports, the *Loligo* fauna of South Africa is singularly poor, only *L. reynauldii* being recorded.

#### *LOLIGO INDICA* Pfr.

One example (♀) from Station 167, Natal Coast; 36 fathoms.

Undoubtedly referable to this Indo-Malayan species. A small female sexually mature and measuring 67 mm. in dorsal mantle-length. The suckers (which are affected by sexual dimorphism) of the sessile arms correspond to Goodrich's description (1896, p. 7), there being six teeth on the largest sucker (v. Massy, l.c. p. 220).

Sub-order 2. **Octopoda.**Tribe 1. **Incirrata.**Family **POLYPODIDÆ.**Sub-family **ELEDONINÆ.****VELODONA** Chun.

This genus was founded by Chun for the reception of a species of polypod obtained by the 'Valdivia,' which resembles *Moschites* in the possession of a single row of suckers on the arm, but differs from it in the possession of (a) a funnel organ composed of two separate pieces, (b) a sigmoid bend in the hectocotylized arm, and (c) the development of extensive lateral membranes on the arms.

The present example is, as previously stated (Robson, 1924 a, p. 206), of uncertain age. The fact, therefore, that the hectocotylus does not show the sigmoid bend described by Chun cannot be used as evidence, though we have shown that there is some suggestion that it has attained its definitive form. I am a little sceptical whether the bend itself is of any value taxonomically, as it may be the result of the contraction of the brachial membrane.

Some additional information is given here which enables us to make the position of this genus a little more clear. The funnel organ resembles *Moschites charcoti* and *brevis* (Massy, 1916, pp. 154 & 159) in its general structure, and is fairly close to the thick, clumsy type of the former. It is also like *Scœurgus tetracirrhus* in general but not *S. uniccirrhus*. It is unlike the northern *Moschites* and *Polypus*. The funnel itself offers no particular divergence from the latter genera. The hectocotylus is open to doubt. If the condition in Chun's specimen is constant, it is certainly unique. The velum, again, is unique, but not altogether unfamiliar among polypod genera. The suckers suggest *Moschites*. The radula is peculiar, with the inclination towards *Polypus*, but the line between the latter and *Moschites* is not clear. The mandible is somewhat *Polypus*-like. The *genitalia*, if anything, tend to resemble *Moschites*. Thus, out of eight characters, three are like *Moschites*, two like *Polypus*, one inclines towards *Polypus*, and one is probably unique. The balance is therefore slightly in favour of relationship with *Moschites*, and, owing to the similar funnel organ, with the southern forms of that genus.

**VELODONA TOGATA** Chun, var. **CAPENSIS** Robson.

*Velodona togata* Chun, 1915, p. 480.

" " var. **A**, Robson, 1924 a, p. 206.

Four specimens: 2 (♂) from Stn. 99, Natal Coast; 220 fms.

1 (♂) " " 396, " " 250 "

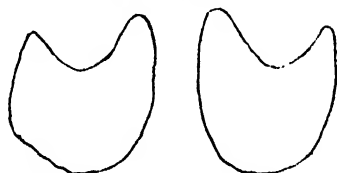
1 (♀) " " 162, " " 240 "

The external features have been already described.

The *funnel organ* is not figured in Chun's description. He says, "jeder Abschnitt besteht aus zwei breiten Lappen" (*l. c.* p. 484). (For the form, *cf.* text-fig. 30 and discussion above.)

The "*funnel articulation*" is strongly developed on the funnel side, the outer edge of the basal fold rising up in two peaks as in *Polypus* and *Eledone*. It is very difficult to understand how these peaks actually act as a locking apparatus analogous to that

Text-figure 30.



*Velodona togata*. Funnel organ.  $\times 2.3$ .

found in the *Egopsida*, *e. g.* They are themselves weak though relatively deep, and seem to have absolutely nothing with which to engage on the mantle side.

The *mandibles* (text-fig. 31) are of the ordinary Polypod shape. They do not agree very closely with either *Moschites charcoti* (Massy, *l. c.*), *cirrosa* (Isgrrove, 1909, fig. 27), or *Polypus*, though they come nearer some forms of the latter in the shallow gular lamina of the lower mandible.

The *radula* is characterized by the absence of lateral cusps on the rhachidian tooth (*cf.* *Bathypolypus*, *infra*), though occasionally vestiges are seen. This feature is also found in *Moschites* (*M. sp.*, Massy, *l. c.* p. 160).

Text-figure 31.



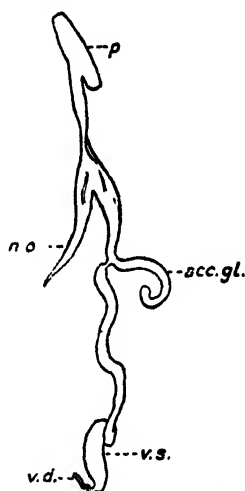
*Velodona togata*. Mandibles.  $\times 1.5$ .

The first laterals are very wide, and the second laterals in one specimen exhibit a "heel" found in both the allied genera.

The *reproductive organs* ( $\delta$ ).—Marchand (1907, p. 357 *et seq.*) figures only those of *Scaurgus* and *Polypus*, extended so as to show details. Those of *Moschites aldrovandi* etc. are figured, but in the case of the adult they are not fully displayed. Massy figures in detail *M. turqueti* and *charcoti*.

The main features agree with *Moschites* and *Polypus* pretty closely. Needham's organ is smaller, but this may be an effect of age. There is a prominent glandular swelling on the vas deferens, which is situated very much as in *M. charcoti* (Massy, l. c. fig. 12). The accessory gland is scarcely dilated at its

Text figure 32.



*Velodona togata*. Male genitalia.

acc. gl., accessory gland; p., penis; v. d., vas deferens; v. s., vesicula seminalis.

extremity, a feature in which it tends to resemble *Moschites*. The penis is cylindrical and has a small posterior appendix. The aquiferous duct is well-developed; it originates from the anterior surface of the gonad near the point of origin of the vas deferens.

#### Sub-family OCTOPODINÆ.

Grimpe (1921, p. 300) has proposed the separation of this sub-family into a number of genera, some of which he has not yet defined, though he has designated types of the genera. Among these are *Bathypolypus* and *Benthoctopus*. According to Grimpe, the first of these includes *arcticus* Prosch (the type-species), (?) *faeroensis* Russ., *lentus* Verrill, and *obesus* Verrill. The second includes *piscatorum* Verrill (the type) and *ergasticus* P. & H. Fischer (= *profundicola* Massy (cf. Massy, 1909) and ? = *sponsalis* Fischer). I assume that what Dr. Grimpe has in view is the contrast between the form exemplified in *arcticus* in which the hectocotylus is large and massive, and in *piscatorum* in which it

is slender and more normal. Examination of the radula of an undoubted *piscatorum* ('Challenger,' Brit. Mus.) and of the figure of *arcticus* (= *bairdii*) given by Verrill (1882, p. 395) shows likewise a marked contrast in that the rhachidian tooth of the former is multicuspid, that of the latter unicuspid, while characteristic differences are likewise found in the lateral teeth. *Faeroensis* Russel, with regard to these characters of hectocotylus and radula, clearly goes with *arcticus* (cf. Russel, 1922, figs. 4 & 5). The radulae of *lentus* and *obesus* are unknown. *Ergasticus* is clearly a difficulty. Its hectocotylus (Fischer & Joubin, 1906, pl. xxii. figs. 1 & 2) is not of the broad massive type seen in *arcticus*, but, though it is small, its parts are more differentiated than those of *piscatorum* (cf. Massy, 1909, pl. ii.). On the other hand, the radula has a unicuspidate rhachidian tooth (Massy, l. c. p. 8). The two forms described below are distinguishable by the characters of the radula. In the case of *B. grimpei* the radula and hectocotylus obviously connect it with the same group as *arcticus*. *B. berryi* is only represented by a female, but its radula is clearly of the *piscatorum* type. Its skin is quite smooth, in which it agrees with the latter and differs from *grimpei*, *arcticus*, *faeroensis*, etc.

We may add the latter character to our list of generic differentia. As to other characters on which to base these genera, I am quite at a loss, as none offer any well-defined and maintained differences. The gelatinous or muscular condition of the surface-tissues of the mantle break down in the case of *grimpei* and *berryi*, in which they are both gelatinous.

### BENTHOCTOPUS Grimpe.

Abyssal polypods with small hectocotylus, multicuspid rhachidian teeth, and smooth skin. There is no ink-sac. Type: *B. piscatorum* (Verrill).

#### BENTHOCTOPUS BERRYI, sp. n. (Plate II. fig. 7.)

One specimen (♀) from Stn. 524, S.W. Cape Town; 1200 fms.

#### Dimensions.--

Total length;	260 mm.
Mantle-width;	47 "
" length from apex to edge of umbrella, between dorsal arms;	108 "
Length, level of eyes to umbrella edge (dorsal arms);	62 "
Interocular width;	47 "
Nuchal width;	38 "

	R.	L.
Minimum depth of umbrella, arms 1-1 ;	45	
" " " " 1-2 ;	45	45
" " " " 2-3 ;	50	48
" " " " 3-4 ;	45	45
" " " " 4-4 ;	36	
Length of arms, 1st pair ;	—	185±5
" " 2nd "	—	188
" " 3rd "	170	173
" " 4th "	160	158

### *Head and mantle.*

The appearance of this region of the body is very striking, the only form which resembles it being *Polypus leioderma* (Berry, 1910, p. 288).

The mantle is rounded and globular apically. It is very short, the transverse width exceeding that of a line drawn from the apex to the posterior corner of the eye. There is a very clearly-marked nuchal constriction, beyond which the ocular region expands to the same width as the visceral sac. The eyes are very large and globular, and below them again is a second, less accentuated constriction. The ocular area constitutes approximately three-quarters of total mantle and head region.

The anterior and posterior regions of the body are completely smooth.

The colour is generally a light purplish brown, which is deeper ventrally than dorsally, a rather unusual feature. In the region of the "neck" it becomes paler, and ceases abruptly in the dorsal and dorso-lateral region just above the eyes. The ocular swellings and the dorsal surface of the umbrella are quite pale, being very faintly tinted by a light scattering of pigment spots.

The first pair of arms bears sixty-six pairs of suckers preceded by three unpaired ones. The sucker pairs are arranged diagonally, and the paired condition is continued to the tip of the arm.

### *The funnel.*

The funnel organ is W-shaped (text-fig. 33). Its four limbs are equal in length and thickness, measuring 4.5 mm. across. The orifice of the funnel has on its anterior side an infolding, suggestive of a valve (text-fig. 33).

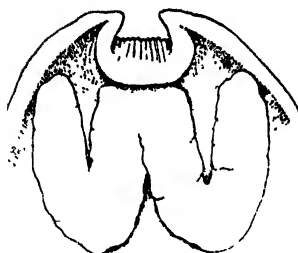
### *The mantle cavity.*

The renal papillæ are long, measuring 5 mm. The oviducal orifices open at the same level as, and immediately adjacent to, the former.

The gills have eight filaments, exclusive of the azygous terminal one. The branchial hearts are very large, measuring  $9 \times 12$  mm., or practically as large as the gills themselves. The hypobranchial gland is similarly well-developed, and measures 5 mm. in depth.

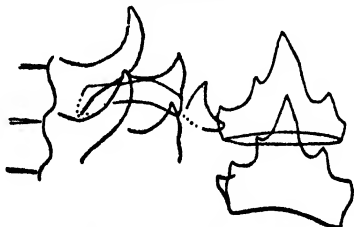


Text-figure 33.

*Benthoctopus berryi*. Funnel organ.  $\times 1.75$ .*The Alimentary System (text-fig. 35).*

The *radula* (text-fig. 34) is remarkable for the decided asymmetry of the median tooth. This asymmetry has been previously figured (*cf.* Massy, 1916, figs. 7, 15). I believe it is of frequent occurrence in polypods, but I have never seen a discussion on its occurrence and significance. In itself it is so remarkable as to merit a full examination. It consists in the regular change of position of the lateral cusps, so that a cusp that is on the

Text-figure 34.

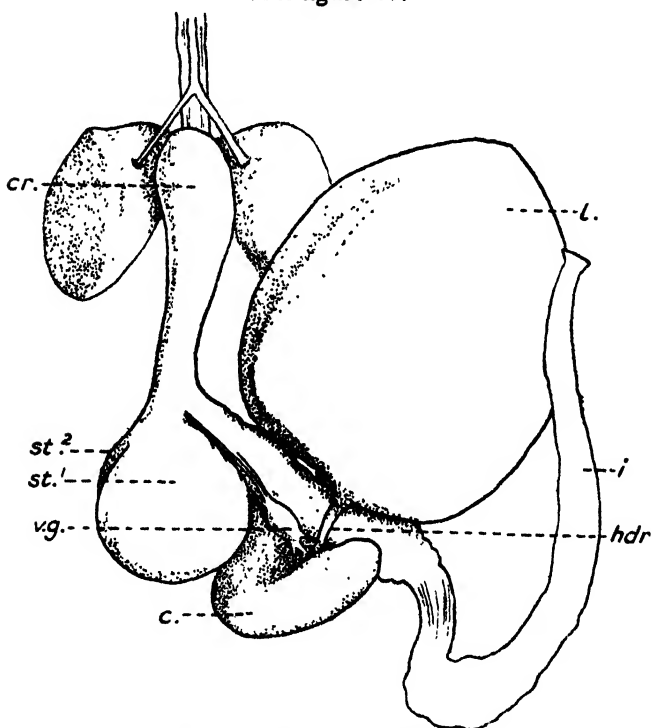
*Benthoctopus berryi*. Radula.  $\times 22$ .

inside in an older tooth eventually finds itself external in a younger tooth. This change of position is asymmetrical, in that it does not take place in the same rhythm on each side of the teeth. We may indicate it by a cusp-formula for a series of teeth. In this A=the unchanged median cusp, and III. and II. the number of lateral cusps. In a typical series the formulæ of successive teeth are:—

L.	R.
III. A . II.	
II. A . III.	
II. A . III.	
III. A . III.	
III. A . II.	
III. A . II.	
II. A . III	

The admedian tooth has a shallow base and a strongly-developed cusp. The second lateral on the inner side slopes steeply to the base without a shoulder. The marginals are very degenerate and are barely perceptible. It is conceivable that they are soluble in potash, and were therefore lost during the preparation of the radula, but this is not very likely. No marginals are figured by Massy for *P. ergasticus* (1909, pl. i. fig. 2). The posterior salivary glands are roughly triangular, and have their

Text-figure 35.

*Benthoctopus berryi*. Alimentary canal.

cr., crop; c., caecum; hdr., hepatic duct; i., intestine; l., liver;  
v.g., visceral ganglion.

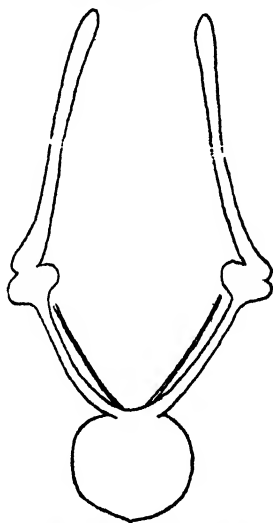
flattened bases posterior in position. The ducts fuse just in front of the crop. The latter is fairly well-developed. The oesophagus is stout and thick. The stomach is divided into two portions (text-fig. 35, *st*<sup>1</sup> & *st*<sup>2</sup>). These are distinguished by the different arrangement of the fibres of the external muscular sheath. The spiral caecum is large and very little twisted. Towards its base it receives the two fused hepatic ducts. The first part of the intestine

is thin-walled. Just after the cæcum is given off, it becomes abruptly narrower and more muscular for a short distance; after which it again becomes thin-walled and wide. There is no ink-sac. The liver is rather heart-shaped.

*The genitalia* (text-fig. 36).

The ovary was small and obviously immature. The proximal part of the oviduct is a third the size of the distal part. The oviducal glands are well-developed. Aquiferous ducts were present, but that on the left side was very slender and filamentous.

Text-figure 36.



*Benthoctopus berryi*. Reproductive system (♀).  $\times 2.25$ .

*Affinities.*

In general outward appearance *B. berryi* is not unlike *P. levis* Hoyle (Southern Ocean, Heard Id., Kerguelen). It differs in the following features:—

A. In *levis* the ratio of the mantle and head to the total length is 100/190; in *berryi* it is 108/260.

B. In *levis* the suckers appear to be biserial from the beginning of the arm; in *berryi* the first three suckers are uniserial.

C. In *levis* the siphon extends to barely one-third of the way towards the edge of the umbrella; in *berryi* it extends half-way towards the latter.

D. The visceral sac is elongate in *levis*; in *berryi* it is round and the ocular area is much larger.

The anatomy of *levis* being unknown (the whole of the adult 'Challenger' specimen was not preserved), it would be rash to assume that it is referable to *Benthoctopus*. At the same time it must be noted that we do not at present know the limits of this genus. For example, we do not know if it is restricted to the North Atlantic species included by Grimepe.

In outward appearance this species has also something in common with *piscatorum* Verrill. The following differences, however, are to be observed :—

(1) The colour in Verrill's species is lighter posteriorly, has a characteristic white band on posterior surface (? absent in Massy's specimen), and is not evanescent on the head.

(2) The ocular masses are only half the size of the visceral sac in *piscatorum*; in *berryi* they are more than half.

(3) The infra-ocular stricture is far more marked in *berryi*.

(4) The arrangement of transverse ridges on the arms seen by Massy in her specimen (1909, p. 14) is absent in *berryi*.

(5) The web is more equally developed in *berryi* than in *piscatorum*.

(6) In Verrill's figure and also in that of Massy of *piscatorum* the eyes are practically midway between the apex of the visceral sac and the edge of the umbrella; in *berryi* they are very much nearer the apex.

(7) Verrill figures rather prominent eyes for his species. 'Challenger' specimens, which otherwise agree very well with *piscatorum*, have more or less normal eyes, and Massy's specimen is similar. In *berryi* the most striking thing are the prominent ocular masses.

#### BATHYPOLYPUS Grimepe.

Deep-water polypods with broad and long hectocotylus and unicuspidate rhachidian teeth. The skin is usually covered with warts, and may be gelatinous. There is no ink-sac. Type: *B. arcticus* (Prosch).

BATHYPOLYPUS GRIMPEI Robson. (Plate II. fig. 10.)

*B. berryi* Robson, 1924 a, p. 207.

One specimen (♂) from Station 405 (Natal Coast); 470 fathoms.

Seven specimens (3 ♂, 4 ♀) from Station 164 (Natal Coast); 380 fathoms.

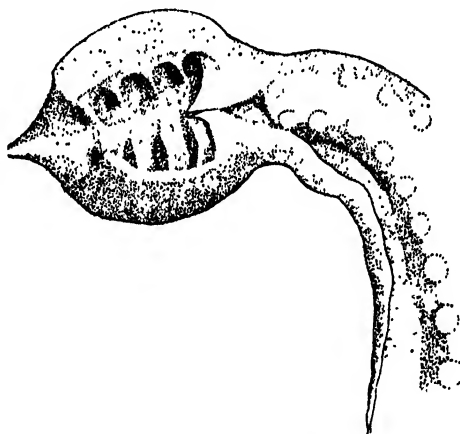
This form has been already sufficiently described so far as its external features are concerned. In the present instance it is enough to add a description of the suckers and some of the internal features.

The suckers are arranged in alternating pairs, the alternation being always apparent at the second sucker. There are 114

suckers in all (maximum) on the longest arms. They are usually very deeply retracted. There is generally the width of a sucker between each successive member of the series, though in some cases they are more widely spaced distally. The last 4 to 5 pairs are usually crowded. Transverse ridges of the arms are found, and the edges of these may be apparent as folds; but this is not a constant feature, and may be due to shrinkage.

The *hectocotylus* (text-fig. 37) has already been described. It makes its appearance in young males of 50 mm. long (or one-third the size of the sexually mature form described here) as a clearly differentiated area with the transverse bars indicated, but no calamus and no infolding. In the form of 60-65 mm. the calamus

Text-figure 37.



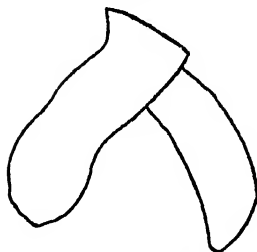
*Bathypolypus grimpei*. Hectocotylus.  $\times 225$ .

is seen, and the whole organ is expanded beyond the width of the arm so as to look like that of *faeroensis* in outline. But in this case the bars are less apparent than in the younger specimen. It is noteworthy that one of the characters which differentiates this species from the others, viz. the deepness of the cup, is not seen at this stage.

#### *Digestive System.*

The mandibles are erect (text-fig. 38). The inferior pair are markedly different from those of *B. arcticus* in the vertical direction of the rostral lamellæ and the small size of the beak. The superior mandibles also differ from *arcticus* in the vertical line of the anterior edges of the palatal lamellæ (cf. *P. bairdii* Verrill, 1880, pl. xii.).

Text-figure 38.

*Bathypolypus grimpei*. Mandible.  $\times 3.25$ .

The *radula* (text-fig. 39). The rhachidian teeth are unicusped and have shallow bases. The latter are very much broader than those of *arcticus* (= *bairdii* Verrill, l. c.). They differ likewise from those of *faeroensis* (Russel, 1922, fig. 5).

The second laterals are likewise different and highly characteristic. There are no fully-developed marginals.

Text-figure 39.

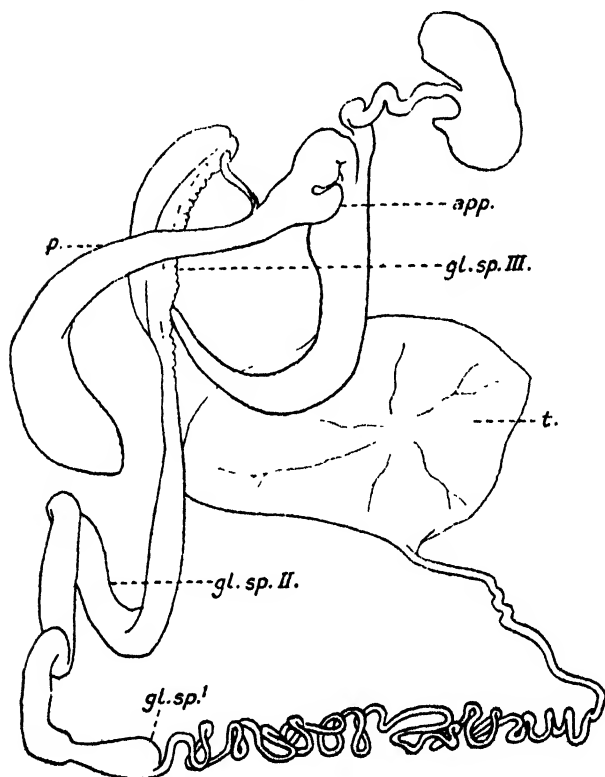
*Bathypolypus grimpei*. Radula.  $\times 50$ .

The crop is rather small. The upper part of the oesophagus enters it in the main axis and in the same line as that in which the lower part leaves it, whereas in most polypods the upper part enters the crop eccentrically (cf. Meyer, 1913, fig. 30). The stomach consists, as in *B. berryi*, of two parts distinguished by their outer surface. The cæcum is scarcely coiled and is blunt and knob-like. The hepatic ducts are long (14 mm.); they seem to enter the cæcum at the point where it curves over. The first section of the intestine is thin-walled. It is succeeded by a more muscular part, which is continued to the anus. There is no ink-sac.

*Reproductive Organs (♂). (Text-fig. 40.)*

The testis and other organs were fully developed and occupied a very large part of the visceral sac, the gills and their appendages being displaced in a *dorsal* direction, and crushed in between the sac and the wall of the mantle. The testis is of the usual general shape. The proximal part of the vas deferens is

Text-figure 40.

*Bathypolypus grimpei*. Generative organs (♂).  $\times 2$ .

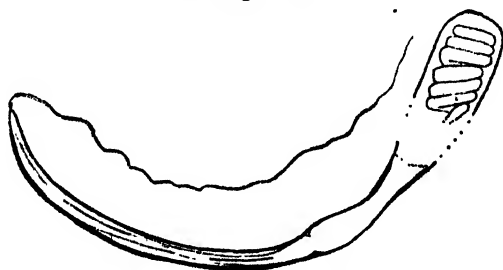
*gl.sp.* I., II., III., vesicula seminalis; *app.*, appendix of the prostate (*p.*);  
*t.*, testis.

very long, measuring about 130 mm. It would appear to be longer than usual, though authors do not usually specify the length of this structure. The second part is likewise very long (96 mm. ?+4). It consists of (1) a short glandular portion (*gl. sp. i.*; cf. Marchand), (2) a thin-walled part, and (3) a long glandular section (*gl. sp. ii. & iii.*). One area of this is transversely

ribbed like the prostatic part of the spermooviduct of a pulmonate. The prostate is long, and very much expanded distally. Its neck is long and thin. There is a well-marked accessory gland at its proximal end. Needham's organ is long and pointed. The penis has a well-marked posterior diverticulum. The system as a whole is very like that of *B. arcticus* (Prosch, 1849, fig. 1, pl. i.). The first part of the vas deferens is longer, and the prostate is of a different shade from the club-like form seen in *arcticus*. The *diverticulum penis* is not so long and pointed in the latter.

The *spermatophores* measure about 35 mm. Employing the terminology used by Russel (1922, p. 30) and based on that of Racovitza, we may distinguish the aboral end as very much swollen (5 mm. diam.). The region of the false tube is also swollen. The oral tube expands somewhat below its extremity. The flagellum measures some 40 mm.

Text-figure 41.

*Bathypolypus grimpei*. Spermatophore.  $\times 2.5$ .

The structure (text-fig. 41) is like that of *B. arcticus* in the swollen aboral extremity, but Prosch's figure is otherwise very unsatisfactory. The swelling seen at the level of the false tube in *grimpei* is not figured by Prosch, and on the other hand I do not find the twisted length of oral tube shown in his figure (2a).

This species has marked affinities with *P. valdiviae* Chun (1915, p. 485), and at first sight it was identified with that form. On close study it was found, however, that scarcely any system exhibited real resemblance. The following table shows the facts on which the distinction is based:—

## VALDIVIAE.

## GRIMPEL.

- |  |   |
|--|---|
| 1. Head very wide, width across eyes exceeding that of mantle. | Head normal, ocular width about the same as that of mantle.   |
| 2. A long cirrus over the eyes.                                | Surface sculpture like that of <i>valdiviae</i> , but cirrus not present in adult, though indicated in young. |



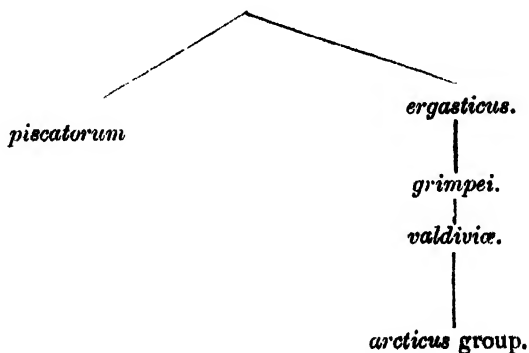
## VALDIVIÆ.

## GRIMPEI.

- |   |   |
|---|---|
| 3. Colour red-brown on dorsal, clear brown on ventral surface.          | Colour less differentiated on dorsal and ventral surfaces. General shade (formalin specimen) dull purplish brown. |
| 4. Mantle "breiter als hoch" (but cf. figure).                          | The reverse.  |
| 5. Funnel organ well-developed.   | Absent in adult; very occasionally found in undeveloped condition in young.                                       |
| 6. Hectocotylus: (a) with five "querwulste"; (b) tip rounded and bent.  | Hectocotylus: (a) with four "querwulste"; (b) tip pointed and more or less straight.                              |
| 7. Radula (cf. fig. 39 and Chun, l. c. fig. 53).                        |   |
| 8. Locking apparatus of mantle includes a deep cleft below mantle-edge. | No cleft.   |
| 9. Apex of mantle rounded.  | Apex of mantle usually drawn to a pronounced point.   |

Chun (l. c. p. 455) has compared *P. valdiviæ* with Joubin and Fischer's *ergasticus* and *sponsalis*. It has already been pointed out that *ergasticus* cannot be accommodated in Grimpe's two genera, as it combines a unicuspid rhachidian tooth with a small (though differentiated) hectocotylus.

I think the truth is probably that, from the normal hectocotylus to the large massive type, we have a series of graded types, and that the differentiation of the rhachidian tooth does not in all cases keep pace with that series. Thus *ergasticus*, which has a fairly small hectocotylus, has a completely unicuspid rhachidian. It will be thus seen that a hard-and-fast generic arrangement in such a case and with such data is out of the question. As far as relationship is concerned, the following diagram may provisionally be used:—



This diagram indicates that the combination of the radular character and increase of size and complexity of the hectocotylus qualify *ergasticus* for the line that gave rise to the *arcticus* group; but in view of the size of the hectocotylus and the amount of upward folding of the sides, which is less than in *grimpei* and *valdiviæ*, it may be considered as less specialized. *Sponsalis* is excluded from this table as nothing is known of the radula.

The foregoing remarks seem to stress the northern affinities of *grimpei* and *valdiviæ*. There are some indications that similar forms may be found among the deep-water polypods of other parts of the world (e.g. *P. hoylei* Berry, 1912, p. 298); but I am inclined to think that the affinities of these species are as indicated, though it must be admitted that the evidence is, as yet, very incomplete.

#### BATHYPOLYPUS ? VALDIVIÆ (Chun).

One specimen (♂), immature, from Station 63 (Cape Town); 220 fathoms.

A very young example, probably referable to this species.

#### POLYPUS RUGOSUS (Bosc).

? *Sepia rugosus* Bosc (1792, p. 24).

Three examples: 2 ♀ (Nos. 1 & 2) from Stn. 388 (Natal Coast); 38 fathoms.

One ♂ (No. 3) from Stn. 389 (Natal Coast); 40 fathoms.

In his list of recent Cephalopoda (1886, p. 216) Hoyle has distinguished *P. tuberculatus* D'Orb. as a West Indian, Mediterranean and West African species, and *P. granulatus* Lamarck (= *P. rugosus* Bosc) as an Atlanto-Pacific form. Most workers have accepted this view, but it is evident that a good deal of confusion exists as to the identity of the two forms and to the names which should be applied to them.

The matter is to be dealt with more fully elsewhere, but it is desirable to give a brief resumé here.

Comparison of the examples named "*rugosus*" by Massy (1916, p. 147) from Rio de Janeiro and an example labelled "*granulatus*" from Port Elizabeth (Brit. Mus.) with the Natal examples here described and other Indian Ocean material prove that they differ very fundamentally in the character of the radula and hectocotylus. Certain other structural details differ, but they are not absolutely correlated with the differences just mentioned, and, as far as the *external* characters are concerned, the differences between the Atlantic and the Indian Ocean and Pacific forms are very obviously transgressive. It is extremely dubious what the correct names of the two forms should be. The view that *tuberculatus* (auctt.) is the N. & S. Atlantic and W. African form and *rugosus* the Indo-Pacific form seems to me incorrect; and I am very doubtful whether *rugosus* extends out of the Atlantic at all. As for the actual names to be employed, I think it may be

necessary to adopt the view (1) that de Blainville's *tuberculatus* is the same as the *rugosus* of Bosc, (2) that D'Orbigny (1835, p. 45), misled by the extremely puzzling transgression in external characters, unwarrantedly took Indo-Malayan forms into his *rugosus*, (3) that *rugosus* is the correct name for the restricted Atlantic form, and (4) a new name must be sought for the Indo-Pacific species.

The following data relate to the Natal forms:—Nos. 1 and 2 are purplish brown in colour. There is a marked reticulation on the umbrella at the base of the arms. The bases of the suckers are bright violet in colour, and there is a sharp colour contrast on the inside of the arms (*cf.* Brock, 1887, p. 607). No. 3 is similar but duller in colour.

The skin is covered in all three specimens with small low warts, tending to form lines and occasionally becoming trifid. The ventral surface is finely granular. There is no ventral fissure. The arms are three times as long as the body, and the following formulæ are found:—

No. 1: 3.4.2.1	No. 2: 4=3.2.1	No. 3: 2=3.4.1
3.4.1	4.1.2.3	2.4.1

The brachial membrane is only slightly developed, and the umbrella is practically absent between the first arms. The *hectocotylized* arm has a small distal apparatus. This is wider than the 'Terra Nova' "*rugosus*," the calamus is much more blunt, the ligula is adjacent to the last sucker, and the whole arm is very short. The beak of the inferior mandible is very short. In the

'Text-figure 42.



*Polypus rugosus*. Radula. Admedian teeth.  $\times 32$ .

radula (text-fig. 42) the cusp of the admedian tooth is at the exterior angle, while the second lateral is devoid of an entocone. Comparison of text-fig. 42 with text-fig. 5 of Massy's 1916 paper will show the marked difference between the Natal and Brazilian forms.

#### *Undetermined Polypods.*

1. One specimen (? sex) from Station 46, west of Cape Town; 260 fathoms.

A very young specimen (mantle 17 mm. long), very like young *B. grimpei*, but with the anterior and posterior surfaces of the mantle sharply demarcated by a ridge, as in *B. aroticus*.

2. One specimen (? sex) from Station 294 (?); 260 fathoms.

A young example (mantle-length 18 mm.) in unsatisfactory condition.

This specimen is very remarkable in the possession of suckers arranged singly out to the edge of the umbrella, after which they become biserial for a short distance and finally uniserial again. In general appearance it is not unlike a young *B. grimpei*.

## Family BOLITÆNIDÆ.

### ELEDONELLA Verrill.

The status of this genus and of the associated *Bolitæna* has always been a source of confusion. In 1920, Sasaki (1920, p. 170) proposed to cut the Gordian knot by placing *Bolitæna* (of Chun, 1911), *Japetella* [part] (Hoyle, 1885), and *Eledonella* (cf. Hoyle, 1886) as synonyms of a new genus, *Chunella*, on the ground that *Bolitæna* was a name given to a genus closely related to *Alloposus*. Actually the description of *Bolitæna* given by Steenstrup was very incomplete. Hoyle (1886), who had had access to Steenstrup's MS., reproduced (l. c. p. 16) a fuller description of *B. microcotyla*. In 1884, Verrill had described *Eledonella pygmaea* the type of a new genus, and in this genus Hoyle placed his *diaphana* (1886). Chun and Thiele referred the latter, however, to *Bolitæna* (1914 and 1915). In 1918, Joubin (1918, p. 40), after a consideration of the central nervous system, separated *Bolitæna* (*B. diaphana* Hoyle [sic!]), *Eledonella* (*E. pygmaea* Verrill), and *Vitreledonella* (*V. richardi* Joubin).

I do not think we are in possession of enough material yet to solve the whole of this difficulty. I venture, however, to submit evidence that clears up a certain part of the difficulty; though, if it is accepted, another one is immediately raised. As Berry (1921, p. 352) points out, Sasaki's contention that *Bolitæna* (cf. Steenstrup and Hoyle) is an *Alloposus*-like form needs elaboration; but I may point out two facts that render Sasaki's view very plausible. In 1904, Hoyle described specimens of *B. microcotyla* from the 'Albatross' collection. He figured the radula and described the funnel organ. He also (v. p. 11) compared his example with one in the Hamburg Museum "closely resembling Steenstrup's type." Neither the radula nor the funnel organ is at all like that of *E. diaphana* or *pygmaea* (auctt.) and would be considered generically distinct (cf. his fig. 1, pl. iv. of the radula and description of the funnel organ (p. 9) with the figures of *diaphana* and *pygmaea* in Chun (1915)). In short, the W-shaped funnel organ resembles that of *Alloposus mollis* (cf. Berry, 1912, text-fig. 12), and the radula with its tricuspid rhachidian and unicuspidate laterals again resembles that of *A. mollis* (cf. Joubin, 1895, pl. v. fig. 11) rather than that of *diaphana* etc. If, then, we agree that the form described by Steenstrup has nothing to do with *diaphana* etc., but that it is probably to be applied to an

*Alloposus*-like form, what is the relation of *diaphana* to the type-species of *Eledonella*? Is there any justification for regarding it as generically distinct (cf. Chun and Joubin)? In spite of the important differences in the central nervous system described by Joubin, I am a little inclined to discount it taxonomically. The radulae of the two forms, though offering some contrast in the number of denticles of the lateral teeth, do not appear to be generically distinct, nor are they in their other features so much dissimilar. As to the value of the character of the central nervous system, on which Joubin relies, I may point out that *E. massyæ*, which in general is near *diaphana* and *pygmæa* and is certainly distinct generically from *Vitreledonella* on the radula, agrees with the latter in the characters of its nervous system, and not with the former.

One point remains for consideration. If we accept the evidence adduced above, and, on account of its resemblance to *Alloposus*, reject *Bolitana* from association with the *Eledonella*-forms, we are almost compelled *ipso facto* to reconsider the status of *Alloposus*. *Bolitana* would have some twenty years' priority over *Alloposus*, and would have to replace it. However, although I am satisfied that there is some evidence that the *Bolitana* of Steenstrup is not congeneric with *diaphana* etc., I do not think we know enough about it to say it is with certainty identical with *Alloposus*.

*ELEDONELLA MASSYÆ* Robson. (Plate II. fig. 8.)

*E. massyæ* Robson, 1924 a, p. 202.

One specimen (♀) from Station 87 (Cape Town); 1014 fathoms.

The external features of this species have already been described (Robson, *l. c.*), but some additional details may be given. The ground-colour in formalin was a pale yellow. The surface was covered with numerous rich purplish-brown chromatophores, which tend to fuse on the head and arms to give a purplish tint. The colour of *diaphana* and *pygmæa* (v. Chun) is characterized by the presence of bright orange-red chromatophores.

The dimensions of the umbrella are as follows (measurements being taken from the level of the first sucker, which lies about the same level as the point at which the arms separate):—Between arms 1-1, 9 mm.; arms 1-2, 7 mm.  $\pm$  1; arms 2-3, 7.5 mm.; arms 3-4, 6  $\pm$  1; arms 4-4, 0 mm.

The suckers, which, as in *diaphana*, are imbedded in a membrane on some of the arms, are slightly globular and are devoid of any definite constriction.

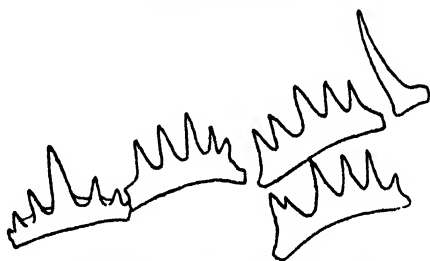
In the original description it was stated that *massyæ* differs from *diaphana* in its widely-spaced suckers. All the accounts of *diaphana* agree in showing the suckers closely serried, except in the case of the very young specimen figured by Joubin (1900, pl. ii. fig. 6), in which on two of the arms the suckers seem more widely spaced than usual. I am inclined to discount this, owing to the size of the specimen and the possibility that the drawing

may be inaccurate. It should be noted that the number of suckers on each arm in adult specimens of *diaphana* far exceeds that found in *massyæ*. The proportions of the visceral sac exhibit some differences from *diaphana*. I am a little inclined to mistrust evidence based on such a plastic character. But the fact remains that the width of the mantle-aperture relatively to the maximum width of the mantle is distinctly less than in all the described or figured examples of *diaphana*. The proportions likewise attained by the umbrella between the various arm-pairs differ in general from those exhibited in *diaphana*, though there is agreement in detail. More noteworthy differences from *diaphana* in funnel organ, radula, and central nervous system are described below.

It remains to note that additional differences from *E. heathii* are found in the absence of definite constrictions of the suckers and in the lack of prominence in the eyes.

The statement under A (2) in my original paper (1924 a, p. 203) requires some qualification with regard to the head, in which I now consider very little size-difference can be seen. Similarly,

Text-figure 43.



*Eledonella massyæ*. Radula.  $\times 35$ .

the size of the head renders it less unlike *pygmaea* than I originally thought (cf. Chun, pl. lxxxi. fig. 5). The radula (cf. Thiele, 1915), central nervous system (Joubin, 1918), and the spacing of the suckers, on the other hand, are strong points of difference from Verrill's species. Neither Verrill nor Chun represents *pygmaea* as having the suckers joined by a membrane.

The funnel organ is very unlike the triangular structure figured by Thiele (l. c. p. 494). It is broadly V-shaped, with the arms of the V rather leaf-shaped and its apex rounded. Within the mantle-cavity the funnel is continued to a considerable depth by its lateral retractor, which forms two long "bridles" which are inserted on to the body-wall along their entire length.

The median septum terminates apically on a level with the branchial hearts. This septum is composed of two sheets of tissue, which are inserted in the body-wall some distance right and left of the median line. The gills and branchial hearts are supported on a wide ligament similar in distribution to that of

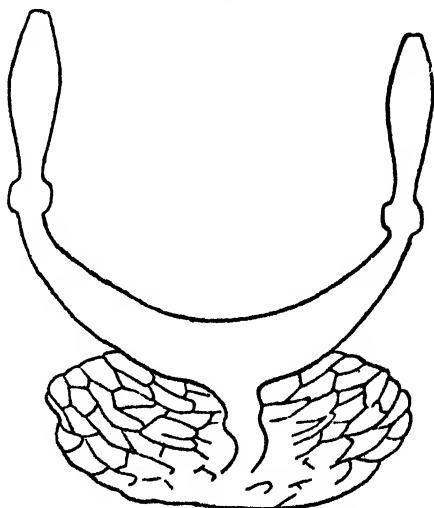
*E. diaphana*. The integument covering the viscera is covered, as in the latter species, by a number of large pigment spots.

The *radula* (text-fig. 43).—The rhachidian tooth has usually a tall median cusp and three lateral cusps on each side. There seems to be a serial repetition (v. p. 660), in which at every fourth tooth the admedian lateral cusp occupies a position as a sort of outgrowth from the main cusps (cf. both *pygmæa* and *diaphana* Thiele, 1915). The tooth as a whole seems to be intermediate between the two latter species, and differs from *diaphana* in its relatively narrow base. The first laterals are five-cusped. The tooth is perhaps more like that of *diaphana*, but the cusps are longer and more slender. The second laterals are five- to six-cusped, with a serial tendency for the first cusp to be double at every fourth tooth. These teeth again are more like *diaphana*, but the number of undivided cusps exceeds that of the latter.

#### *The Circulatory and Respiratory System.*

The heart is asymmetrically placed on the dorsal side of the reproductive organs. It is more triangular than pear-shaped (Chun, 1915, p. 520). There are two arteries coming off independently at the ventral end, instead of three arising from a

Text-figure 44.



*Bludonella massyæ*. Female reproductive system.  $\times 5$ .

common trunk (as in *diaphana*). The genital artery arises in the same position as in *diaphana*, while the origin and course of the cephalic artery resembles that species.

The branchial hearts are very large relatively to the size of the

gill. On the dorsal surface is found a very small "appendage." This is not noticed by Chun (1915) or Joubin (1918).

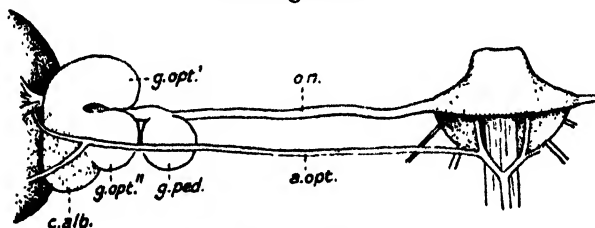
The pallial vein bifurcates immediately after passing the gills as in *E. diaphana*.

There is a well-developed branchial gland as in *Vitreledonella* (Joubin, 1918). This organ is not described by Chun for *diaphana*, but in his fig. 5, pl. lxxxiii. a structure is shown that may represent it.

The *Reproductive Organs* (text-fig. 44) have already been briefly characterized (Robson, l. c. p. 203). No trace of an aquiferous duct was found, and it is not referred to in *Vitreledonella* by Joubin (l. c.).

The *Nervous System* (text-fig. 45).—The optic nerve is very long. The peduncular ganglion is situated close up against the optic ganglion as in *Vitreledonella*, and not in the middle of the optic nerve as in *Eledonella pygmaea* (cf. Joubin, 1918, p. 40). There are two distinct optic ganglia of approximately equal size, and adherent to the lower is a corpus album (of a dark grey colour).

Text-figure 45.



*Eledonella massyae*. Optic ganglia.  $\times 7$ .

a.opt., optic artery; c.alb., alb. corpus; g.opt. I, II, optic ganglia; o.n., optic nerve.

This is present in *E. diaphana*, but not in *pygmaea*. In *Vitreledonella* the optic ganglia are fused or single, between the optic and peduncular ganglia is a minute "tache grise ovale," while on the eyeball itself is a "corps blanc." These constitute marked differences between Joubin's genus and this form, and may be set off against the resemblance in the position of the peduncular ganglion.

On the whole the affinities of this form are distinctly with *pygmaea* and *diaphana*, though with which of these forms it should be compared is uncertain. *Pygmaea* is probably more definitely northern in the Atlantic, while *diaphana* ranges from north of the Equator in the Atlantic to the Indian Ocean and Pacific. There can be no question of the distinctness of *E. massyae* from *diaphana* in many characters. Though this species is founded on a single female, the majority of the differentia are not such as usually have a sexual basis. Hoyle's type is almost unrecognizable. What is available for study (the arms and suckers to wit) is unlike our form.



Tribe 2. *Cirrata*.

## Family CIRROTEUTHIDÆ.

## CIRROTEUTHIS Eschr.

This group of animals and the allied *Stauroteuthis* have long been a source of confusion. As it is treated at present, it contains a number of forms of very dubious affinity. Verrill (1880, p. 382), Hoyle (1886, pp. 55 & 59), Berry (1910, p. 271), and Grimpe (1916, p. 326) have all either speculated on the relationships of the two genera or proposed grounds for separating them.

The two most definite pronouncements are those of Berry and Grimpe. They characterize the two genera thus:—

Stauroteuthinæ—*Stauroteuthis*: dorsal cartilage horseshoe-shaped.  
Cirrroteuthinæ—*Cirrroteuthis*: „ „ saddle-like.

Verrill was of the opinion that the open or closed condition of the mantle-cavity was of taxonomic importance; but this important feature has not been considered by later authors.

After reviewing the description of the nineteen or twenty species that are assigned to these genera, I find myself totally out of agreement with Berry and Grimpe. As Joubin points out (1920, p. 21), the shape of the dorsal cartilages is most inadequate for taxonomic purposes. The animals in question cannot be divided into two even moderately distinct groups on the strength of this character. In *C. mülleri* and *magna* the cartilage is saddle-like. In *meangensis* it is rectangular, and hoop-like (Hoyle, 1886, pl. xiii, figs. 5 & 6). In *hippocrepium* (*ibid.* 1904) it is rounded and like a narrow horseshoe. In *grimaldii* (Joubin, 1912) it resembles a wide half-hoop. In *ebersbachii*, *syrtensis*, and the present species it is V-like. It is true that the form seen in the first two is not found in the others; but among the latter there is just as wide a difference between (*e. g.*) *meangensis* and *ebersbachii*. In other words, the criterion of distinctness breaks down on this character. Again, the mantle-aperture is equally fallacious as a guide. We find it widely open in *megalope* Berry, partly open in *mülleri*, closed in *grimaldii*, etc.

These two characters cannot be correlated, as the correlation breaks down in the case of *massyæ* and *magna*, which have a saddle-like cartilage and closed mantle-cavity. Otherwise the horseshoe-like cartilage is found, with the closed condition of the latter.

I would also point out that other evolutionary tendencies are at work that are not expressed in the distinction quoted above, and may be important:—A. There is a line of descent leading to forms with the fins placed apically on the mantle (*e. g.* *grimaldii*) and a short, squat visceral sac. B. There are forms in which the visceral sac is small and the arms and velum progressively longer. There are, however, such large gaps in our knowledge (*e. g.* the shape of the dorsal cartilage is known accurately in only ten out

of eighteen species), that it is useless to speculate on the true arrangement of these forms. In such a position I consider it the more reasonable and sounder taxonomic principle to avoid the erection of artificial groups where the evidence is so unsatisfactory. As a case in point, the present species is in general not unlike Grime's *Chunioteuthis ebersbachii*, which the author likens to *Stauroteuthis syrtensis* on the strength of its V-shaped cartilage. But it seems to me that the characters on which Grime's genus rests would qualify nearly all the known species to be given separate generic status.

There would be in the present instance a case, as a palliative, for maintaining *Stauroteuthis* and *Cirroteuthis* for at least the extreme forms, e.g. those combining a saddle-like cartilage with an open mantle (e.g. *mülleri*), as opposed to those with a hoop-like cartilage and a closed mantle (e.g. *syrtensis*). But in actual fact, so few forms have crystallized out into these combinations or any satisfactory generic character-complexes, that one has no option but to fall back on the original type-genus of the family and await the advent of more information. Exactly the same conclusion is arrived at by Joubin (*l. c.*).

*CIRROTEUTHIS GILCHRISTI* Robson. (Text-fig. 46.)

*C. gilchristi* Robson, 1924, p. 204.

One adult (♂) from Station 526 (Cape Town); 1400 fathoms.

A few details may be added to the description of the external parts. A fresh examination has confirmed the impression that the species has some affinities with *Chunioteuthis ebersbachii* (Grime, 1916, p. 357), though it is very distinct specifically.

1. The fins are more or less parallel-sided and rounded at the outer end, not triangular as in Grime's species. They are about the same length as in the latter.

2. The measurement of the arms is very doubtful, as the amount of error due to their elasticity is very large. Their tips are not all complete.

3. The fragile umbrella membrane is broken in many places, and its extent is very uncertain. The following depth measurements are approximate:—

Between arms 1-1 .....	115 mm.
1-2 .....	115 "
2-3 .....	— "
3-4 .....	— "
4-4 .....	105 ? "

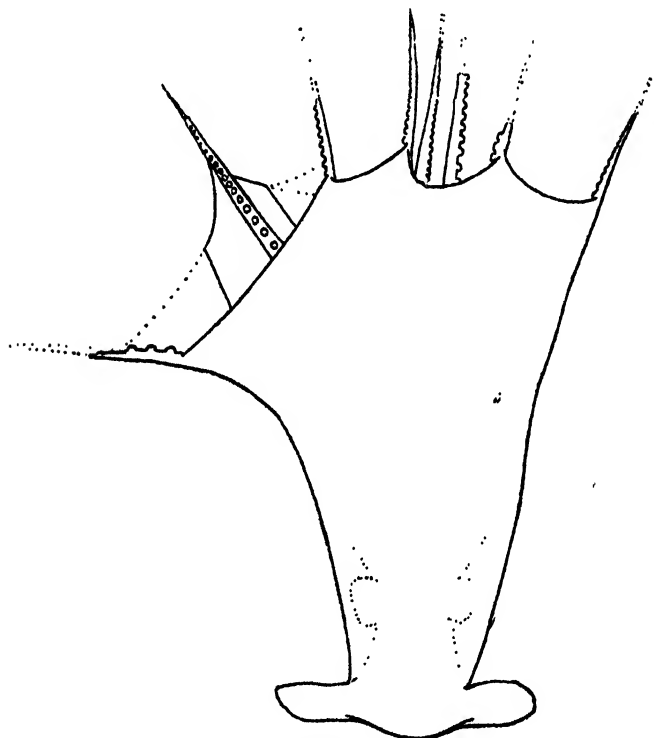
4. The cirrhi measure anything up to 18 mm. in length, and are therefore shorter than those of *ebersbachii*.

5. The profile of the suckers differs from that of *ebersbachii*, in which the first two are "spitzkegelig," the next fourteen to sixteen "stumpfkegelig," the first four being knob-like, and in succeeding ones flatter and far less conical.

6. The first four suckers differ very markedly in form and size from the succeeding ones, and there is a rapid change in size between the fifth and seventh.

7. The mantle-orifice is reduced to a small pore, from which the funnel does not project. This is an important character, probably of generic value. It agrees with *egersbachii* in this respect. It is probable that in neither case is the funnel extrusible.

Text-figure 46.



*Cirroteuthis gilchristi*.  $\frac{1}{2}$  nat. size.

The *hectocotylus* is very little known in the genus. Grimpe (1916, p. 358) supposes that the enlargement of the suckers in the proximal region of the arms may represent this. Sasaki (1920, p. 169) states that in *S. albatrossi* both dorsal arms are hectocotylized, being provided with three very conspicuous suckers half-way along their length. I am myself a little sceptical as to whether a slight enlargement of suckers is a sign of hectocotylization (*cf.* the condition in the female *Semiroessa*), though there seems to be some evidence that substantial enlargement in

some species of *Polypus* is at least sex-limited (cf. Robson, 1921, p. 437).

The dorsal cartilage (text-fig. 47) is remarkably flat (not resembling that of *C. umbellata* as originally stated), and seems to foreshadow the practically straight form seen in *Opisthotenthis*.

#### *Pallial complex.*

When the mantle-cavity is opened, the general disposition of the viscera is seen to be different from that found in *St. wülkeri* or *Ch. ebersbachii* (Ebersbach, 1915, pp. 370-371). The cavity is very much reduced, occupying only about one-half the width of the visceral sac. The fusion of mantle and head has evidently been extended apically to the restriction of the cavity. As a result all the pallial organs are very much crowded. The funnel has a considerable free portion, and is extended so as to cover the anus, and is secured to the ventral body-wall along the median line. On its inner side is a paired funnel organ situated very high up near the anus.

The gills have eight (there are nine in *ebersbachii*) main lamellæ. The branchial gland ("Kiemenmilz") projects beyond the gill

Text-figure 47.



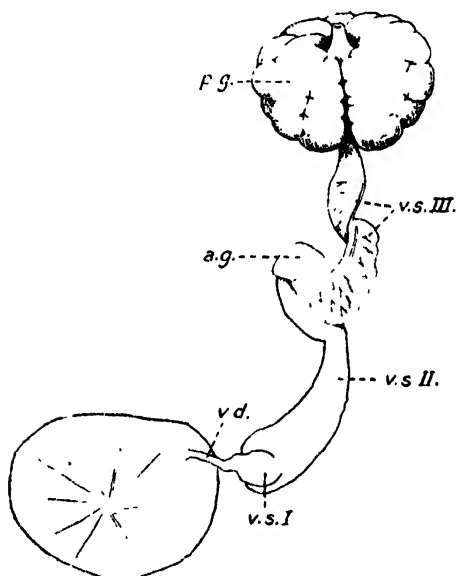
*Cirroteuthis gilchristi*. Dorsal cartilage.  $\times 2.4$

apically, and there is a large circular branchial heart. On the dorsal surface of the latter is a small circular appendage. The heart is markedly asymmetrical and rather unlike that of *wülkeri* (= *umbellata* of Ebersbach, l. c. pl. ix. fig. 4). It resembles that of *Opisthotenthis* (cf. Meyer, 1906, pl. xiii. fig. 14) more nearly. The genital artery and posterior aorta come off a common trunk. The pallial artery divides into a superior and lateral branch, of which the latter supplies the fins. The anterior aorta curves anteriorly and downwards, giving off a branch to the liver and then following the usual course.

*Genitalia* (text-fig. 48).—The testis was median in position and well-developed. There is a very short proximal vas deferens, which abruptly enlarges into the first seminal vesicle. At the junction of the third and second seminal vesicles is a small accessory organ, probably equivalent to the accessory gland of *C. wülkeri* (*umbellata* [sic] Ebersbach, text-fig. 17). The third seminal vesicle runs direct into the very large penial accessory gland, in the centre of which is the short penis. The second seminal vesicle is thin-walled; the third muscular. Needham's organ was found on the anterior surface of the accessory penial

gland. There is a certain general resemblance between this form and *ebersbachii* and *wülkeri*. It is, if anything, nearer the former, from which it differs in characters already discussed (Robson, 1924, p. 205). In *ebersbachii*, moreover, there is practically no distinction between the first vas deferens and the first seminal vesicle. In this our species resembles *wülkeri*, which it again resembles in the possession of an accessory gland.

Text-figure 48.

*Cirroteuthis gilchristi*. Male genitalia.

*a.g.*, accessory gland; *p.g.*, accessory gland of penis; *v.s.*, vesicula seminalis;  
*v.d.*, vas deferens.

A second individual from an unknown station is probably referable to this species. It is in a damaged condition, and while its general form, fins, and genitalia seem to resemble those of *gilchristi*, the dorsal cartilage is bent at a more acute angle and the adoral suckers are not enlarged.

#### CIRROTEUTHIS A.

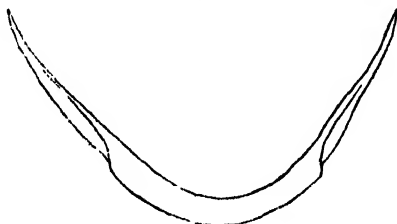
Three specimens from Station 525 (Cape Town); 1000 fathoms.

Eight " " 526 ( " " ); 1400 "

These specimens are nearly all very small, about 40 mm. long. One only measures over 60 mm. Inasmuch as not even in the largest is the gonad mature (judged by its small size relatively to the containing capsule), I assume that the examples are not mature, and therefore undeserving of a specific name.

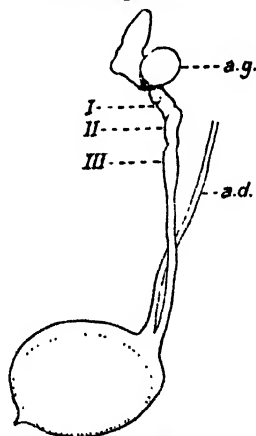
The animal has the same general shape as *C. grimaldii* Joubin and *Stauroteuthis* sp. (young) (Berry, 1910, p. 274)—i. e., it is short and squat, with a thick umbrella extending far up the arms, and apical fins. It differs from the latter and from *ebersbachii* and *gilchristi*, however, in having a relatively large mantle-orifice,

Text-figure 49.

*Cirroteuthis* A. Dorsal cartilage.  $\times 5.33$ .

and from the latter in having the fins less terminal in position and the cartilage more U-shaped and more like that of *C. ebersbachii*. The shape of the cartilage (text-fig. 49), the position of the fins, and certain characters of the funnel differentiate it from *wülkeri*,

Text-figure 50.

*Cirroteuthis* A. Male genitalia.  $\times 7.57$ .

a.g. ? = accessory gland of penis; a.d., aquiferous duct;

I, II, III ? = rudiments of vesicula seminalis.

while many characters differentiate it from the young *umbellata* described in the original account of that species (Fischer & Joubin, 1906, p. 320). The mantle-aperture is roughly one-third the width of the visceral sac. The fins are large, narrow at the base, and somewhat expanded distally.

The arms are subequal in length, and measure about 48 mm. in the largest specimen. The average number of suckers is 50. They show a tendency to increase in size up to the ninth, after which they decrease again. The cirrhi are small, measuring not more than 1 to 1.2 mm., and extend practically to the end of the arms. They are plainly retractable into crypts, which, at least in the adoral region, have well-marked muscular walls.

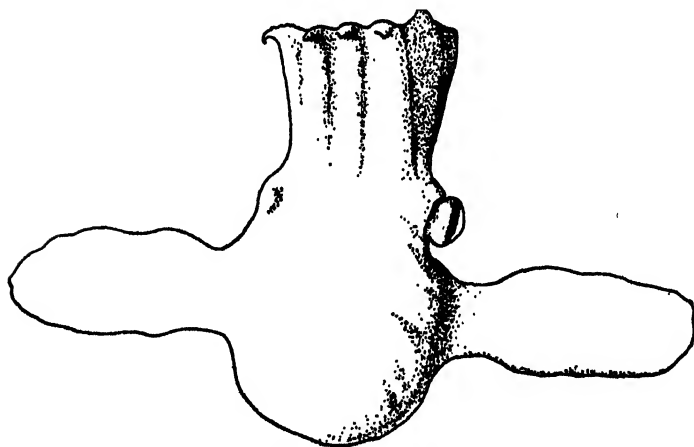
*Genitalia*.—Three males were examined, and all were found to be in an undeveloped condition (text-fig. 50), the characteristic structure of this group being undifferentiated. A well-developed (?) accessory gland of the penis was found. The aquiferous duct was likewise well-developed.

(*CIRROTEUTHIS* B. (Text-fig. 51.)

One example (immature) from Station 85; 790 fathoms.

This specimen only measures 14 mm. over all, and is in all probability immature.

Text-figure 51.



*Cirroteuthis* B.  $\times 4$ .

Owing to the possibility of its being a form of *C. umbellata* and to the consequent importance of the external form, it was considered undesirable to dissect the animal.

We are not possessed of any exact data as to the external expression of juvenile characters in this genus, so that the following points may be useful:—

A. The cirrhi are represented by low, rounded papillae in this form. In the small *meangensis* (30 mm.) the cirrhi are small, but not exactly papilliform. It is a question whether the papilliform condition of the cirrhi in this case is specific or merely due to

immaturity. Unfortunately there are available no records of actual specimens of young examples between 14 and 30 mm. In Fischer's youngest example the cirrhi are not described, and are not visible from the figure. Among the young examples of *Cirroteuthis* A (*v. supra*), one measuring some 29 mm. has short but definite cirrhi. The same is true of Berry's *S. mawsoni* (32 mm.). The result is that we are unable to say whether the papillae in this case are early stages of cirrhi or definitive structures.

B. More positive information is available as to the length of the arms relatively to that of the umbrella.

In this form the arm-tips are barely clear of the top of the umbrella, a condition seen in Berry's *mawsoni* (Berry, 1917, figs. 1-3) and *Stauroteuthis* sp. (*ibid.* 1910, pl. xxxiii. fig. 1.). In young and old examples of *Cirroteuthis* A we find the following figures:—

	Total length (1).	Tip of arm to edge of umbrella. (=x.)	$x \times 100$ length
1 ... ..	60 mm.	19	31
2 ... ..	45 „	11.5	24
3 ... ..	42 „	12	28
4 ... ..	39 „	10	25
5 ... ..	32 „	8	25
6 ... ..	32 „	7	21
7 ... ..	32 „	6	18

We thus have a steady increase in the length of  $x$  with increasing total length, which indicates that the present example is possibly juvenile. It should be pointed out, however, (1) that in all fairly young specimens, though the umbrella is continued up the arms, the former at least in one case (*umbellata*, cf. Fischer, 1906, pl. xxv. fig. 10) is deeply indented; and (2) that one cannot always safely argue from size to age.

The fins are relatively enormous, and are long and paddle-like, recalling the condition seen in *O. megaptera*. The umbrella and arms are remarkably short. The dorsal cartilage is distinctly horseshoe-shaped, recalling those of *umbellata* and *wülkeri* (Grimpe, 1920, p. 237). From the latter this form is distinguished by the following characters:—

- (1) The fins are relatively larger and of a different shape.
- (2) i. The funnel is acorn-shaped at the end in *wülkeri*; while it is tubular in this case (*cf.* Grimpe, 1920, fig. 5).
- ii. The orifice of the funnel is anteriorly directed in *wülkeri*, posteriorly in this case.
- iii. The inferior border of the funnel and the taste-organs are within the mantle-cavity in *wülkeri*, and outside it in this case.
- iv. *wülkeri* possesses a *foveola*-like depression which is absent in this form.



From *umbellata* it is distinguished by (1) the size and shape of the fins; (2) the greater freedom of the funnel from the head in *umbellata* (Grimpe, l. c. fig. 5 b, B); (3) the shape of the funnel, which is intermediate between *wülkeri* and *umbellata*; and (4) the dorsal cartilage, which is distinctly more angular than that of *umbellata* (Grimpe, l. c. fig. 4).

From *megaptera*, which it resembles in the size of the fins, it is distinguished by (1) the absence of the very deep indentation at the insertion of the fin, (2) the shape of its fins\*, and (3) its short umbrella region. I understand from Joubin's account that he satisfied himself that *megaptera* has a horseshoe-like cartilage.

On the whole I am inclined to think that this form is probably very immature, but that it is a distinct species with affinities among the North Atlantic forms.

It may be noted that the right eye of this form was almost burst from its socket.

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\* The resemblance to *megaptera* in this respect is only general.

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## EXPLANATION OF THE PLATES.

### PLATE I.

- Fig. 1. *Abralia gilchristi* Robson. Type. Natural size.  
 2. *Octopodoteuthopsis* sp.  $\times \frac{1}{2}$ .  
 3. *Anomalocranchia impennis* Robson. Type.  $\times \frac{1}{5}$ .  
 4. *Rossia enigmatica* Robson. Type.  $\times \frac{2}{3}$ .  
 5. *Liocranchia intermedia* Robson. Type.  $\times \frac{1}{4}$ .

### PLATE II.

- Fig. 6. *Sepiella cyanea* Robson. Type.  $\times \frac{1}{2}$ .  
 7. *Benthoteuthis berryi* Robson. Type.  $\times \frac{2}{3}$ .  
 8. *Eledonella massya* Robson. Type.  $\times \frac{1}{2}$ .  
 9. *Rhombosiepien hieronis* (♀) Robson. Cotype.  $\times \frac{1}{2}$ .  
 10. *Bathypolypus grimpei* Robson. Type.  $\times \frac{2}{3}$ .  
 11. *Rhombosiepien hieronis* (♂) Robson. Cotype.  $\times \frac{1}{2}$ .

27. The Necessity for Quantitative Methods in the Investigation of the Animal Life on the Sea-bottom. By C. G. JOH. PETERSEN, Ph.D., LL.D., D Sc., Copenhagen \*.

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#### SUMMARY.

The method hitherto followed in the study of the fauna of the sea-bottom of establishing zoogeographical regions is defective and suffers from several radical faults. It should be supplemented and in time superseded by the new method of establishing the "communities" or characteristic faunas of smaller areas. This community work has been rendered possible by the elaboration at the Danish Biological Station of special instruments, and in particular the bottom sampler or grab, by means of which the quantitative abundance of the animals living at or in the bottom can be determined and the areas of occurrence of the different communities charted out. The charting of communities has been successfully achieved in the Skager Rack, Kattegat, and Belts, but much remains to be done in more open waters, such as the North Sea and the Norwegian Sea. Widespread quantitative investigations giving a trustworthy conception of the number of animals per unit of bottom must be carried out, if any real progress is to be made in the study of the zoogeography of the sea. When the communities have been charted out in the manner indicated, we shall have a better and more reliable picture of the distribution of life on the sea-bottom than has been achieved by any other method.

The ordinary method of marine zoogeography has hitherto consisted in an enumeration of the species belonging to the various systematic groups found in certain water; further, in comparing the number of species in one area with that in another, and thus enabling one to draw up "provinces," "regions," or what other designation one happens to prefer.

Further, zoologists have tried to ascertain the distribution of each species everywhere in the sea, in order to draw conclusions as to the external conditions under which the different species live, and where to look for their "centres of distribution."

This system has originated within the walls of museums, and, as a rule, it is founded on more or less casual sampling. Seldom have the collector and the specialist been the same person, and

\* Communicated by Dr. E. S. RUSSELL, F.Z.S.

necessarily the more common animals have been left out of the collections on account of limited space. Specialists have treated the different systematic groups with next to no co-operation. Further, they have hardly ever tried to get a distinct general view of all the species found together in the different areas\*. Probably it would not have amounted to much in any case, methods and implements for the enumerating of animals from the sea-bottom having always given misleading results.

We must not blame the zoologists for the present situation, "botanizing" out at sea is a very expensive affair and not within the means of everybody. Once I myself worked along these old lines, endeavouring though to keep within the limits of one small area, i. e. the Kattegat. However, I, as well as the others, lost sight of "the general view."

It is easy to understand, then, that zoogeographers from time to time have been tempted to make purely physical conditions the basis of their investigations, particularly the depth, the temperature, and the degree of salinity, as at least some knowledge could be obtained of these matters. But it has since been ascertained that, with regard to the conditions required by different species, no theory can be laid down in advance, the various life conditions being far too complicated.

The usual terms of zoogeography are at their very best vague and covered by expressions such as "arctic," "boreal," "lusitanic," "boreoarctic," etc., or "littoral," "sublittoral," "abyssal," "archibenthal," etc., "stenothermal," "eurythermal," etc.; but even for a domain so characteristic as the Arctic regions are supposed to be there has not been obtained a universal definition, either geographically, or by means of temperature, or in any other way.

The above-mentioned system is deficient and suffers from several radical faults. First and foremost all investigators know the difficulty over the identification of different species when extensive material from many parts of the world has to be treated. Further, this identification has in modern days suffered an essential alteration, inasmuch as the "Linnæan species" often can be divided into many smaller species, and to unravel those is very difficult if any great number of marine species is in question. Such a study has not as yet been commenced. The base of the system, the identification of the single species, is therefore not so reliable as it has hitherto been considered.

Besides this, many species are too widely distributed to be characteristic for zoogeographical provinces. I shall only mention the eel, and among the lower animals the Ophiurid, *Ophiocten sericeum*, of which species individuals can be found from the Arctic regions, as far down as the South of Europe, and perhaps still farther south.

Individuals, especially young ones, can be met with far from

\* John Murray in the 'Challenger' Expedition is an exception to the rule.

their proper domain, i. e. far from the waters where the species lives and breeds as a regular thing. *Macra subtruncata*, for instance, is found within the Skaw only in the young stages. And last, not least, it is in itself a very difficult matter to know the whole distribution of a species, a matter that cannot be decided without numerous investigations; it is therefore very unfortunate to have to base our knowledge about the external conditions of any species on this single circumstance.

Without doubt it has always tacitly been taken for granted that any one species requires nearly the same conditions wherever it appears. How far this is true is not possible to decide. When noting in how many different animal communities the different species are found, we cannot help thinking that great powers of adaptation have been given to them.

But the greatest defect of this kind of investigation is the fact that no attempt has been made to describe in broad lines the character of the animal life of the different waters which have been investigated, so that it could be ascertained what species were of the greatest occurrence and, so to speak, characteristic of the different waters. To be sure, we have designations such as "coral reef," "banks of shell," etc., but I hardly believe that zoologists have created these notions.

As a matter of fact, geologists have succeeded much better in their descriptions of extinct faunas by means of species characteristic for different formations. I shall only mention such names as *Yoldia-layers* after *Yoldia arctica*, *Cardium-layers* after *Cardium edule*, *Zirphæa-layers*, *Tapes-layers*, etc.

The geologists have been able to make a true estimation of the fossil animals of the different layers far more easily than the zoologists, as many of these formations are on shore and within easy reach, while zoologists have had nothing but the contents of the dredge to rely upon, and these contents are very capricious and not at all representative.

In Sweden (de Geer) geologists have got so far as to investigate each individual layer and its contents of molluscs and other animal species quantitatively, in order to characterize them. This is the right way to work.

We have thus seen that the present conditions, so unfavourable for zoologists, are, as above mentioned, due not only to the fact that exploration of the sea-bottom is very expensive, but also to the fact that convenient implements have been wanting, implements that could give trustworthy quantitative information about the population of the sea-bottom. Such implements are now to hand, for instance, the bottom sampler or grab, that at least partly solve this problem. By means of bottom samplers it has been possible to determine the species characteristic for different formations, and to indicate their intensity of occurrence per 1 m.<sup>2</sup>, at least on a level sea-bottom.

These implements, for the construction and use of which I refer the reader to the reports from the Danish Biological

Station, particularly Nos. 20-25, were not introduced by me for zoogeographical reasons, but merely in order to determine the amount of fish-food per 1 m.<sup>2</sup> of the sea-bottom. It soon, however, became evident that some areas of the bottom were inhabited by uniform animal life, characterized in each area by a few species of common occurrence. These areas were early designated according to their characteristic species, and looked upon as actual animal communities. In Danish waters they were, as a rule, easy to map out where the sea-bottom consisted of gravel, sand, clay, or a mixture of those substances, but quite suddenly areas of stony ground might appear on the level sea-bottom, and these stony areas were found to possess an altogether different animal population. I have grouped such species as "Epifauna." They are difficult to map out as they generally only appear in patches; we must be content simply to state where we meet with them; hence I shall leave them out of this paper, regarding them as, at least in Denmark, a rather exceptional phenomenon, and I shall keep to the communities of the smooth sea-bottom.

By means of the bottom sampler we soon got evidence about the following facts:—

(1) We determined the numbers of individuals of each species met with in each separate area, all specimens being collected and preserved. When the more common animals, on account of their bulk, were thrown away, their numbers and weight were first recorded.

(2) We accumulated knowledge about the characteristic species by which the community is determined and defined.

(3) We were able at once to refer each bottom sample to its community, and the occurrence of the different communities could be charted during the investigations when the communities had been characterized.

(4) The fauna of such explored water could thus be divided into its characteristic elements. Instead of having everything mixed, and talking about the fauna of the Danish waters as compared, for instance, with that of the Swedish or Norwegian Skaergaard, we start by deciding on the communities which are found in these waters, and then we compare the corresponding communities of the two waters, or we compare waters with corresponding communities. Kristianiafjord, for instance, ought to be likened to the entire Skager Rack, as these areas have almost similar animal communities. On the other hand, the Gullmarfjord is lacking some of the deep-water communities from the Skager Rack, and the Koljefjords communities may best be compared to those of the Greater Belt.

(5) By charting the communities we determine the areas with approximately the same fauna, and thus presumably the same external conditions, and we do it better and easier than by investigating the temperature, the salinity, and other physical

conditions, as the observations of these facts are but few and far between. The occurrence of the different animals determines *ipso facto* where the necessary conditions for them are to be found. These conditions are in reality of a very complicated nature, not only in physical and chemical respects, but also as regards organic factors (*e. g.* competition), and we need not depend on one single species, but have several common ones to judge by. This will probably be the best way to get at a suitable delimitation of areas with similar natural conditions.

(6) In this way we are able by charting to work our way from small domains to greater ones. By means of the community-domains we can without doubt obtain a more natural and more reliable classification of the areas of the sea-bottom as regards their fauna and the conditions of life than has been achieved by any of the older methods. No knowledge obtained by employing the older methods is neglected in going over to the newer community-method, but this method gives much additional information. The new method requires, however, greater labour on the part of the collector and more systematic knowledge of the animal species of common occurrence.

On dry land, botanists have gained fine results by basing the geography of plants on the larger systematic groups of the higher plants, these groups possessing two qualities, *i. e.* their species are highly community-forming, and they do not contain an excessive number of species, and last, not least, systematically viewed, they are thoroughly well-worked groups.

The zoologist also must keep himself within bounds; it is impossible to treat every systematic group at once. Earlier investigations prove that Echinoderms, Molluscs, the higher Crustaceans, and Chætopods play a similar part on the level sea-bottom to that played by Phanerogams on land, so far as species characteristic for the formations are concerned.

I have tried to transfer the system of Raunkiaer and others, of utilizing the ecological types of the plants for characterizing the "plant-climates," to the animal communities in the sea, but without gaining any reliable results. For the moment at least I must keep to the occurrence of the common and characteristic species as determining the communities.

I shall here mention some instances of the abundance of Echinoderms on the sea-bottom. In the Kattegat, for instance, I have taken up to 200-250 *Amphiura chiajei* per 1 m.<sup>2</sup> from the *Brissopsis lyrifera*-*Amphiura chiajei*-community, and up to 19 *Brissopsis* per 1 m.<sup>2</sup> From the *Echinocardium*-*Amphiura filiformis*-community I have taken ca. 3000 *Amphiura* per 1 m.<sup>2</sup> and up to 20-28 *Echinocardium* per 1 m.<sup>2</sup> From the Venus-community I have taken up to 50 *Echinocardium* per 1 m.<sup>2</sup> besides the fry.

I have determined eight different animal communities in the Danish waters on the level sea-bottom, from the shore and out to



the deep water—in the Skager Rack about 700 metres. And I know that several of these communities are to be found outside the Skager Rack, *e. g.* in the North Sea.

My scheme for future investigations is therefore not to give up the enumeration of the different species, but in addition to this to study the animal life on the sea-bottom by means of the species characteristic for the different communities, to endeavour gradually to map out the distribution of the communities based thereupon, and to describe them as precisely as possible, both as to quantity and as to quality. We should then learn which animal species live together at the different parts of the sea-bottom. When the domain of a community has been charted, by means of the bottom sampler, other implements (trawl, dredge, etc.) should be employed, in order to discover the more mobile and rarer animals living in the community.

If it then proves that one or more communities are characteristic, *e. g.* of Arctic regions—and I do not doubt that such communities exist,—then the actual distribution must be taken as a basis for the delimitation of these regions called “arctic,” and they must be charted. The same will be the case with “boreal,” “lusitanic,” and other domains. I doubt, however, whether these charts will have much in common with most of the denominations now in use in marine zoogeography.

I shall here allow myself to refer to a hypothetical chart in Report XXI. from the Danish Biological Station (Supplement to Report XXII.), showing my provisional conception of the limits of some of the said communities\*.

Properly speaking, no charting of communities has been thoroughly done except from the Baltic up to Kristiania and in some parts of the North Sea. Before charting of greater areas has been done, we can hardly tell how many communities there may be and how complicated the orientation will prove to be. The number of communities, however, we may partly control, and should we be forced to simplify matters greatly, the characteristic species of Echinoderms, especially the Ophiurids and the Echinoids, would lead to a good preliminary orientation. They are found in such tremendous numbers on the sea-bottom that we are sure to find several individuals from both groups, or at least from one of them on each 1 m.<sup>2</sup> All investigators ought, therefore, in the future to be well acquainted with the systematics of these groups, especially with regard to the more common species. A fuller knowledge as to the life on the sea-bottom is, of course, obtained by adding the characteristic species

\* Since this was written I have received two papers on bottom sampler work in the North Sea (Ministry of Agriculture and Fisheries, Fishery Investigations, ser. 2, vol. vi. No. 2, 1923, by F. M. Davis; and Fishery Board for Scotland Scientific Investigations, 1922, No 8, by A. C. Stephen). I am able to recognize about four of the Danish communities among the samples published; but, as far as I can see, the bottom in the North Sea is, as a rule, not nearly so densely covered with animals as in the Kattegat; therefore more samples are necessary in the North Sea, if we are to have the communities as well defined as we have in Denmark.

from the other groups. I do not think it will be a hard task to determine the communities characteristic for, say the European "boreal" and "arctic" waters, for the present I must use these general expressions. In suitably chosen places, sections ought to be taken from the coast out to deep water. These sections will be sure to contain most of the communities to be found in these waters. This is what I have done, for instance; in the Skager Rack. A few profiles taken off the West coast of Norway and in Arctic waters would sample the more important communities. How far we should afterwards enter into details in elucidating the conditions of smaller waters is another question.

We must not forget that the bottom sampler works very quickly, almost as if we take a cast of the lead. Many stations can therefore be investigated in one day, provided the water is not too deep. All the communities of the North Sea could in the time of a few weeks be charted on broad lines by means of a suitable ship, and in one summer the necessary lines could be worked along the coast of Norway and in the Arctic regions. In other words, only this short time would be needed for providing a solid basis for characterizing the zoogeographical regions in these waters.

That we already have, especially with regard to the fishes, an idea that characteristic domains are to be found in these regions (Jungersen and Hjort), is accounted for by the fact that the trawl takes fish better than the dredge takes the lower animals living on the sea-bottom, though the number and bulk of these animals are many times greater than those of the fishes. By means of the *bottom sampler* we can, however, get a quicker and more reliable orientation as to the many animals living on the sea-bottom than is obtained by using the trawl among the more mobile and rarer fish. Appellöf's treatise on the animal life of the sea-bottom based upon his great experience of the older investigations is certainly about the best that can be obtained, but his indications are not sufficient, and any kind of charting is lacking. Of great interest is the Swedish expedition to the Isfjord at Spitzbergen, and especially the excellent treatise by N. von Hofsten on Echinoderms with the charting of the distribution of the different species, but he has only made use of the older methods of investigation. Quantitative investigations giving trustworthy conceptions as to the number of animals living on 1 m.<sup>2</sup> of the sea-bottom must be used, if we are to make any real progress in zoogeography by means of the occurrence of characteristic species.

We shall perhaps be forced to use as a basis higher systematic unities than "species," e. g. "genus," "family," etc. It is curious to observe that in Puget Sound on the West coast of North America there appears in shallow waters, dry at ebb, a community of bivalves, very much like our Danish *Macoma baltica*-community from shallow water, of which the characteristic

bivales are *Macoma baltica*, *Cardium edule*, *Mya arenaria*. In Puget Sound this community is said to consist of three *Macoma* species, *Cardium corbis*, the introduced *Mya arenaria* itself, and, further, another bivalve, *Schizothærus nuttalli*; as a matter of fact, quantitative community investigations have already been started there.

One is astonished at the fact that there exists no advanced quantitative knowledge as to animal life on land. Here I may refer to F. Dahl ('Das Plagfenn' by Chorin, Bd. iii. 1912). He calls attention to the fact that no group, as representative as the Phanerogams, is to be found among land animals, and that the entire number of species in the animal communities in one land-domain is usually so overwhelming, and so very imperfectly treated, that the difficulty of describing any local fauna is immense. So far, we must content ourselves with describing as well as possible a few of their Biocoenoses quantitatively. From what I have hitherto seen, I am inclined to believe that it is far easier to get one's bearings as to the animal life on the sea-bottom than on land. All that is required are suitable implements used in the right way.

## EXHIBITIONS AND NOTICES.

March 18th, 1924.

E. G. B. MEADE-WALDO, Esq., Vice-President,  
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of February :—

The registered additions to the Society's Menagerie during the month of February were 66 in number. Of these 36 were acquired by presentation, 16 were deposited, 4 were purchased, 8 were received in exchange, and 2 were born in the Menagerie.

The following may be specially mentioned :—

A Chimpanzee (*Anthropopithecus troglodytes*), from West Africa, presented by Arthur A. Haserick, F.Z.S., on February 9th.

An Ocelot (*Felis pardalis*), from Brazil, presented by George Chalmers, C.M.Z.S., on February 15th.

A Père David's Deer (*Elaphurus davidanus*), from Woburn Park, presented by H.G. the Duke of Bedford, K.G., on February 12th.

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Mr. D. SETH-SMITH, F.Z.S., Curator of Mammals and Birds, gave an exhibition of colour variation in parrots of the genera *Melopsittacus* and *Palæornis*. Of the former he showed skins of the normal green bird, the yellow variety in which the black pigment was absent, the blue variety in which the yellow pigment had been eliminated, and a white bird with faint traces of blue on the rump.

He showed three living specimens of *Palæornis nepalensis*—one, the normal green bird with pink collar on the nape and black stripes on the sides of the neck; a pale yellow specimen with pink eyes, showing the entire absence of black pigment. This lutino variety had been seen on several occasions both in this and other species of *Palæornis*. The third specimen was a remarkably beautiful one of a pale blue colour, the nuchal collar being white instead of pink. The exhibitor believed the bird to be unique. He was indebted to Mr. Alfred Ezra, F.Z.S., for the loan of these two very interesting specimens.

Mr. Seth-Smith also exhibited a number of Fat-tailed Desert Mice (*Pachuromys dupresi*) that had been bred in the Menagerie. From two females twenty-eight young had been born and successfully reared within the last four months.

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Major E. E. AUSTEN, D.S.O., F.Z.S., exhibited, and made remarks upon, a living specimen of the rare Beetle *Coptocycla sordida* Boheman.

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Mr. GEOFFREY SUMMERS exhibited, and Dr. T. G. LONGSTAFF, M.A., F.Z.S., made remarks upon, a series of cinematograph films of animal-life in Spitsbergen.

#### April 1st, 1924.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

After the Papers had been read, the Meeting was adjourned to enable the Fellows present to pay a private visit to inspect the Society's new Aquarium, to be opened to the Public on April 7th.

#### April 15th, 1924.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of March :—

The registered additions to the Society's Menagerie during the month of March were 194 in number. Of these 65 were acquired by presentation, 34 were deposited, 42 were purchased, 28 were received in exchange, and 25 were born in the Menagerie.

The following may be specially mentioned :—

2 Schlegel's Spider-Monkeys (*Ateles pan*), from Mexico, purchased on March 21st.

4 Pandas (*Elurus fulgens*) and 4 Blackbuck (*Antelope cervicapra*), from India, presented by Alfred Ezra, O.B.E., F.Z.S., on March 12th.

1 Collared Goshawk (*Micrastur melanoleucus*), from South America, new to the Collection, purchased on March 29th.

1 Little Blue Heron (*Florida cœrulea*), from Brazil, new to the Collection, presented by Capt. H. S. Stokes, F.Z.S., on March 18th.

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Prof. R. T. LEIPER, M.D., F.R.S., F.Z.S., gave an account of the Parasitological work at the Society's Gardens.

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ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.

February 5th, 1924.

Sir SIDNEY F. HARMER, K.B.E., F.R.S., Vice-President,  
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the months of November and December, 1923.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a series of photographs of Zebras.

The SECRETARY exhibited, and made remarks upon, some photographs of a Chimpanzee and its "nest."

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a piece of ship's timber attacked by Marine Boring Animals.

In the absence, owing to illness, of Dr. N. S. LUCAS, his Report on the Deaths which had occurred in the Society's Menagerie during 1923 was communicated by Dr. G. M. VEYERS, F.Z.S.

Mr. C. TATE REGAN, M.A., F.R.S., F.Z.S., communicated his paper on "Reversible Evolution with Examples from Fishes," which was followed by a discussion.

Miss MARY L. HETT, B.Sc., F.Z.S., gave a *résumé* of her paper on (1) "On the Family Linguatulidæ," and (2) "Zoological Results of the Third Tanganyika Expedition conducted by Dr. W. A. Cunningham, F.Z.S., 1904-1905: Report on the Linguatulidæ."

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\* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

In the absence of the Authors, the following papers were taken as read :—MALCOLM A. SMITH, M.R.C.S., L.R.C.P., F.Z.S., "New Tree-Frogs from Indo-China and the Malay Peninsula"; R. R. MOLE, C.M.Z.S., "The Trinidad Snakes."

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 19th, 1924, at 5.30 P.M., when the following communications will be made:—

E. W. SHANN, B.Sc., Ph.D., F.Z.S.

Further Observations on the Myology of the Pectoral Region in Fishes.

H. C. CHADWICK, A.L.S.

On some Abnormal and Imperfectly Developed Specimens of the Sea-Urchin, *Echinus esculentus*.

ERIC R. LOWE, B.A., M.B., F.Z.S.

On the Presence of Broadbills (Eurylæmids) in Africa.

Dr. CHAS. F. SONNTAG, F.Z.S.

On the Anatomy, Physiology, and Pathology of the Orang-Outan.

The following Papers have been received :—

E. G. BOULENGER, F.Z.S.

On a new Giant Salamander, living in the Society's Gardens.

ROBERT GURNEY, M.A., F.Z.S.

The Larval Development of some British Prawns (Palæmonidae).—I. *Palæmonetes varians*.

LEONARD HILL, M.B., F.R.S.

The Atmospheric Conditions at the Zoological Gardens,  
London.

W. E. LE GROS CLARK, F.R.C.S.Eng., F.Z.S.

The Myology of *Tupaia minor*.

W. J. PHILLIPPS, F.L.S., F.R.G.S.

On a new Genus of Ribbon-Fishes.

B. N. SCHWANWITSCH.

On the Ground-Plan of Wing Pattern in Nymphalids and  
certain other Families of the Rhopalocerous Lepidoptera.

C. W. ANDREWS, D.Sc., F.R.S., F.Z.S.

Note on an Ichthyosaurian Paddle showing traces of Soft  
Tissues.

The Publication Committee desire to call the attention of  
those who propose to offer Papers to the Society, to the great  
increase in the cost of paper and printing. This will render it  
necessary for the present that papers should be condensed, and  
be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should  
be addressed to

P. CHALMERS MITCHELL,  
*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
*February 12th, 1924.*



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

February 19th, 1924.

Prof. J. P. HILL, F.R.S., Vice-President,  
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of January 1924.

A NEW GENUS OF MONKEYS.

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited a series of lantern-slides to illustrate the characters of a new genus of Monkeys, *Presbytiscus*, founded upon the species described by Dollman as *Rhinopithecus avunculus* (Abstr. P.Z.S. 1912, p. 18). *Presbytiscus* resembles *Rhinopithecus* in cranial and facial characters, having a small upturned nose and a long upper lip, thus differing from *Nasalis*; but it differs from *Rhinopithecus* in the structure of the hands and feet, which have digits remarkably long, as in *Nasalis*, the tip of the hallux, when turned forwards, reaching to the distal end of the first phalange of the 2nd digit. In *Rhinopithecus*, as in the Langurs (*Pithecus*), the digits are much shorter, the hallux, when turned forwards, not extending so far as the distal margin of the plantar pad.

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a series of Cinematograph films taken in the Society's Gardens.

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In the absence of the Authors, Dr. E. W. SHANN's paper on "Further Observations on the Myology of the Pectoral Region in Fishes," and Mr. H. C. CHADWICK's paper "On some Abnormal and Imperfectly Developed Specimens of the Sea-Urchin, *Echinus esculentus*," were taken as read.

Mr. N. B. KINNEAR, F.Z.S., gave a *résumé* of Dr. PERCY R. LOWE's paper "On the Presence of Broadbills (Eurylæmids) in Africa."

Dr. CHAS. F. SONNTAG, F.Z.S., communicated his paper "On the Anatomy, Physiology, and Pathology of the Orang-Outan."

The next Meeting of the Society for Scientific Business will be held on Tuesday, March 4th, 1924, at 5.30 P.M., when the following Communications will be made:—

E. G. BOULENGER, F.Z.S.

On a new Giant Salamander, living in the Society's Gardens.

ROBERT GURNEY, M.A., F.Z.S.

The Larval Development of some British Prawns (Palæmonidæ).—I. *Palæmonetes varians*.

W. E. LE GROS CLARK, F.R.C.S.Eng., F.Z.S.

The Myology of *Tupaia minor*.

C. W. ANDREWS, D.Sc., F.R.S., F.Z.S.

Note on an Ichthyosaurian Paddle showing traces of Soft Tissues.

The following Papers have been received:—

LEONARD HILL, M.B., F.R.S.

The Atmospheric Conditions at the Zoological Gardens, London.

W. J. PHILLIPPS, F.L.S., F.R.G.S.

On a new Genus of Ribbon-Fishes.

B. N. SCHWANWITSCH.

On the Ground-Plan of Wing Pattern in Nymphalids and certain other Families of the Rhopalocerous Lepidoptera.

FREDERIC WOOD JONES, M.B.(Lond.), F.Z.S.

The Status of the Kangaroo Island Kangaroo (*Macropus fuliginosus*).

OLDFIELD THOMAS, F.R.S., F.Z.S., and other European Mammalogists.

*Nomina Conservanda* in Mammalia.

W. N. F. WOODLAND, D.Sc.(Lond.), F.Z.S.

On a new Species of Cestode of the Genus *Caryophyllæus* from an Egyptian Siluroid.

C. H. JOH. PETERSEN, Ph.D., LL.D., D.Sc.

The Necessity for Quantitative Methods in the Investigation of the Animal Life on the Sea Bottom.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
February 26th, 1924.





ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

March 4th, 1924.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

Dr. D. H. HUTCHINSON exhibited, and made remarks upon, a series of Cinematograph films of the movements of *Amœba*, *Volvox*, *Porticella*, *Paramecium*, *Plumatella*, and embryo Herrings.

Mr. H. C. BROOKE exhibited, and made remarks upon, a specimen of a "Blue" coloured *Rattus rattus*.

Mr. E. G. BOULENGER, F.Z.S., communicated his paper "On a new Giant Salamander, living in the Society's Gardens."

Mr. W. E. LE GROS CLARK, F.R.C.S.Eng., F.Z.S., gave a résumé of his paper on "The Myology of *Tupaia minor*."

Dr. C. W. ANDREWS, F.R.S., F.Z.S., communicated his paper "Note on an Ichthyosaurian Paddle showing traces of Soft Tissues."

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In the absence of the Author, Mr. R. GURNEY, M.A., F.Z.S., his paper on "The Larval Development of some British Prawns (Palæmonidæ).—I. *Palæmonetes varians*" was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, March 18th, 1924, at 5.30 P.M., when the following Communications will be made :—

THE SECRETARY.

Report on the Additions made to the Society's Menagerie during the month of February, 1924.

GEOFFRY SUMMERS.

Exhibition of Cinematograph films of animal-life in Spitsbergen.

LEONARD HILL, M.B., F.R.S.

The Atmospheric Conditions at the Zoological Gardens, London.

W. J. PHILLIPPS, F.L.S., F.R.G.S.

On a new Genus of Ribbon-Fishes.

B. N. SCHWANWITSCH.

On the Ground-Plan of Wing Pattern in Nymphalids and certain other Families of the Rhopalocerous Lepidoptera.

FREDERIC WOOD JONES, M.B.(Lond.), F.Z.S.

The Status of the Kangaroo Island Kangaroo (*Macropus fuliginosus*).

The following Papers have been received :—

OLDFIELD THOMAS, F.R.S., F.Z.S., and other European Mam-  
malogists.

*Nomina Conservanda* in Mammalia.

W. N. F. WOODLAND, D.Sc (Lond.), F Z.S.

On a new Species of Cestode of the Genus *Caryophyllæus*  
from an Egyptian Siluroid.

C. H. JOH. PETERSEN, Ph.D., LL.D., D.Sc.

The Necessity for Quantitative Methods in the Investigation  
of the Animal Life on the Sea Bottom.

Sir SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S., F.Z.S.

On *Mesoplodon* and other Beaked Whales.

R. I. Pocock, F.R.S., F.Z.S.

Some External Characters of *Orycteropus afer*.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

March 11th, 1924.



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

March 18th, 1924.

E. G. B. MEADE-WALDO, Esq., Vice-President,  
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of February.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, (1) Desert Mice bred in the Gardens, and (2) colour-varieties in the Alexandrine Parrakeet.

Major E. E. AUSTEN, D.S.O., F.Z.S., exhibited, and made remarks upon, a living specimen of the rare Beetle *Coptocycla sordida* Boheman.

Mr. GEOFFREY SUMMERS exhibited, and Dr. T. G. LONGSTAFF, M.A., F.Z.S., made remarks upon, a series of cinematograph films of animal-life in Spitzbergen.

Dr. LEONARD HILL, M.B., F.R.S., communicated his paper on "The Atmospheric Conditions at the Zoological Gardens, London."

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In the absence of the Authors, the following papers were taken as read :—W. J. PHILLIPPS, F.L.S., F.R.G.S., "On a new Genus of Ribbon-Fishes"; B. N. SCHWANWITSCH, "On the Ground-Plan of Wing Pattern in Nymphalids and certain other Families of the Rhopalocerous Lepidoptera"; FREDERIC WOOD JONES, M.B.(Lond.), F.Z.S., "The Status of the Kangaroo Island Kangaroo (*Macropus fuliginosus*)."

The next Meeting of the Society for Scientific Business will be held on Tuesday, April 1st, at 5.30 p.m., when the following Communications will be made :—

OLDFIELD THOMAS, F.R.S., F.Z.S., and other European Mammalogists.

*Nomina Conservanda in Mammalia.*

W. N. F. WOODLAND, D.Sc.(Lond.), F.Z.S.

On a new Species of Cestode of the Genus *Caryophyllæus* from an Egyptian Siluroid.

C. H. JOH. PETERSEN, Ph.D., LL.D., D.Sc.

The Necessity for Quantitative Methods in the Investigation of Animal Life on the Sea Bottom.

Prof R. T. LEIPER, M.D., F.R.S., F.Z.S.

An Account of the Parasitological Work at the Society's Gardens.

The following Papers have been received :—

Sir SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S., F.Z.S.

On *Mesoplodon* and other Beaked Whales.

R. I. Pocock, F.R.S., F.Z.S.

Some External Characters of *Orycteropus afer*.

GUY C. ROBSON, M.A., F.Z.S.

On the Cephalopoda obtained in South African Waters by  
Dr. J. D. F. Gilchrist in 1920-1921.

BASANTA KUMAR DAS, M.Sc.

On the Intra-Renal Course of the so-called "Renal-Portal"  
Veins in some Common Indian Birds.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

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P. CHALMERS MITCHELL,  
*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
March 25th, 1924.





No. 251.

ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

April 1st, 1924.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

Dr. H. A. BAYLIS, M.A., F.Z.S., gave a *résumé* of Dr. W. N. F. WOODLAND's paper "On a new Species of the Cestodarian Genus *Caryophyllæus* from an Egyptian Siluroid."

Mr. J. O. BORLEY, M.A., communicated a paper by Dr. C. H. JOH. PETERSEN, Ph.D., LL.D., D.Sc., on "The Necessity for Quantitative Methods in the Investigation of Animal Life on the Sea Bottom."

In the absence of the Authors the following paper was taken as read :—OLDFIELD THOMAS, F.R.S., F.Z.S., and other European Mammalogists, "*Nomina Conservanda* in Mammalia."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, April 15th, 1924, at 5.30 P.M., when the following Communications will be made :—

The SECRETARY.

Report on the Additions made to the Society's Menagerie during the month of March, 1924.

GUY C. ROBSON, M.A., F.Z.S.

On the Cephalopoda obtained in South African Waters by Dr. J. D. F. Gilchrist in 1920-1921.

BASANTA KUMAR DAS, M.Sc.

On the Intra-Renal Course of the so-called "Renal-Portal" Veins in some Common Indian Birds.

The following Papers have been received :—

Sir SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S., F.Z.S.

On *Mesoplodon* and other Beaked Whales.

R. I. Pocock, F.R.S., F.Z.S.

Some External Characters of *Orycteropus afer*.

R. BROOM, F.R.S., C.M.Z.S.

On some Points in the Structure of the Pareiasaurian Skull.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.

April 8th, 1924.

No. 252.

ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

April 15th, 1924.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of March, 1924.

Prof. R. T. LEIPER, M.D., F.R.S., F.Z.S., gave an account of the Parasitological work at the Society's Gardens.

Mr. GUY C. ROBSON, M.A., F.Z.S., gave a *résumé* of his paper "On the Cephalopoda obtained in South African Waters by Dr. J. D. F. Gilchrist in 1920-1921."

Mr. BASANTA KUMAR DAS, M.Sc., communicated his paper "On the Intra-Renal Course of the so-called 'Renal-Portal' Veins in some common Indian Birds."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, May 6th, 1924, at 5.30 P.M., when the following communications will be made:—

R. BROOM, F.R.S., C.M.Z.S.

On some Points in the Structure of the Pareiasaurian Skull.

D. M. S. WATSON, M.Sc., F.R.S., F.Z.S.

The Elasmosaurid Shoulder-Girdle and Fore-Limb.

The following Papers have been received:—

Sir SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S., F.Z.S.

On *Mesoplodon* and other Beaked Whales.

R. I. Pocock, F.R.S., F.Z.S.

Some External Characters of *Orycteropus afer*.

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*Secretary.*

ZOOLOGICAL SOCIETY OF LONDON,  
REGENT'S PARK, LONDON, N.W. 8.  
April 22nd, 1924.





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